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By

IDA C. MANN

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With a Foreword by

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Published for the *British Journal of Ophthalmology*

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THE THALAMUS OF THE CAT AFTER HEMIDECORTICATION

By WM H. WALLER

Department of Anatomy, University of South Dakota Medical School

Chromatolytic reactions in cells of the dorsal thalamus, following various kinds of lesions of the cerebral cortex, have been used to indicate the existence of fibre connexions between the degenerated parts of the thalamus and the injured parts of the cortex. Very large cortical ablations, such as those to be described, give little information regarding the arrangement of the thalamo-cortical fibres, but are useful in obtaining a comprehensive picture of the origin of the thalamic radiation as a whole: the resulting degeneration may be expected to affect all the cells which have direct ascending connexions to the cortex.

The difficulty attending the removal of the neocortex of a cerebral hemisphere without injuring subcortical structures is considerable, and a perfect operation of this type has not yet been performed. In the experiment of Munzer & Wiener (1902) with a rabbit, large parts of the frontal and occipital lobes were untouched. Franz Nissl (1913) succeeded in preparing an almost completely hemidecorticate rabbit, but injured several subcortical structures, including the tectum. One of the two cats decorticated by Dusser de Barenne and studied anatomically by Brouwer (1920) had no direct lesion of the dorsal thalamus, but the corpora striata were extensively injured and parts of the neocortex were unharmed. Walker (1935) described the thalami of two monkeys from which the cortex was almost completely removed by Dr J. F. Fulton; in both cases there was slight injury to the thalamus at operation. One of the four cats studied by Bard & Rioch (1937) had practically complete decortication and only very slight injury to the thalamus.

The four attempts at hemidecortication[1] described below are similarly defective in certain respects. However, one of them which had incomplete cortical removal was nearly free of subcortical injury, and in two others, although there was some subcortical injury, the ablation of cortex was practically complete. In only one case was there appreciable operative trauma to the thalamus. The group as a whole presents, it is thought, a fair picture of the effects of hemidecortication on the thalamic nuclei of the cat.

[1] The operations, and the work of sectioning and staining the brains, were done while the writer was in the Department of Anatomy of George Washington University Medical School, Washington, D.C. The assistance of Mr George Macatee, of Washington, in preparing the line drawings, is greatly appreciated.

METHODS

The neocortex of one hemisphere was removed from the brain of each of the four animals in a one-stage operation under nembutal anaesthesia. The excision was done with a knife in two cases, and with the Westinghouse Model F endotherm, using a wire loop electrode, in the other two. No attempt was made to fill the gap left by removal of cortex, the reflected temporal muscle simply being drawn up and stitched to the muscle of the opposite side to cover the large opening in the skull. The skin openings were closed with Michel's clips. The behaviour of the animals was observed and recorded during the survival periods, but will not be described in the present paper.

Cat 97 was killed by an intraperitoneal injection of 4 c.c. of paraldehyde 14 days after operation. Cat 98 was in poor condition and was killed by the same method 10 days after operation. Cats 115 and 120 died of infection 11 and 7 days, respectively, after their operations. All four of the brains were perfused with 10 % formalin, but in the case of cat 115 this was not done immediately after death. The brains of cats 97 and 98 were first perfused with normal saline, and the staining was less satisfactory in the sections of these brains than in the two others. All four brains were fixed in formalin, embedded in nitrocellulose, sectioned at 50 microns, and stained with cresyl violet.

DESCRIPTION OF LESIONS

Cat 97. All of the neocortex except the frontal lobe, the gyrus cinguli, and the ventral part of the temporal lobe, was removed from the right side (Fig. 1). The gyrus proreus, parts of the pre- and postcrucial gyri, and the cortex along the diagonal sulcus and the ventral part of the coronal sulcus, were unharmed, but, as shown in the most rostral section in Fig. 1, the lesion cut deeply into the white centre of the frontal lobe and probably severed many of the fibre connexions of these gyri. Most of the fibres of the gyrus cinguli were cut away, although the limbic cortex itself is well represented in the sections. There was a small cut into the gyrus cinguli of the left side, not sufficiently extensive to produce observable degeneration in the left thalamus. A small amount of occipital cortex remains, but the caudal tip of the hemisphere, back of the most caudal level shown in the figure, was completely destroyed. The remaining part of the right side of the brain was distorted, bulging dorsolaterally so that the caudate nucleus and thalamus were attenuated. Only the extreme dorsolateral tip of the head of the caudate nucleus was injured. There was a small cut (not illustrated) along the lateral side of the internal capsule medial to the globus pallidus, which probably cut some fibres of the corpus striatum. The thalamus was injured by a small diagonal cut near its rostral pole.

Cat 98. The caudal part of the occipital lobe was untouched and a large block of temporal cortex remained, but the frontal pole of the brain on the right side was completely removed. Its place in the sections (Fig. 2) is taken by a mass of fibrous tissue which crossed the midline and filled part of the left

ventricle, extending into the preoptic part of the hypothalamus. The thin rostral part of the septum pellucidum was destroyed, but the direct injury to the contralateral (left) caudate nucleus was negligible. Small bits of cortex containing normal cells remained attached to the lateral side of the connective tissue mass. In sections through the rostral part of the thalamus the injury is seen to involve the lentiform nucleus, but the inrolled hippocampus which covers the caudal part of the thalamus was only superficially injured. The

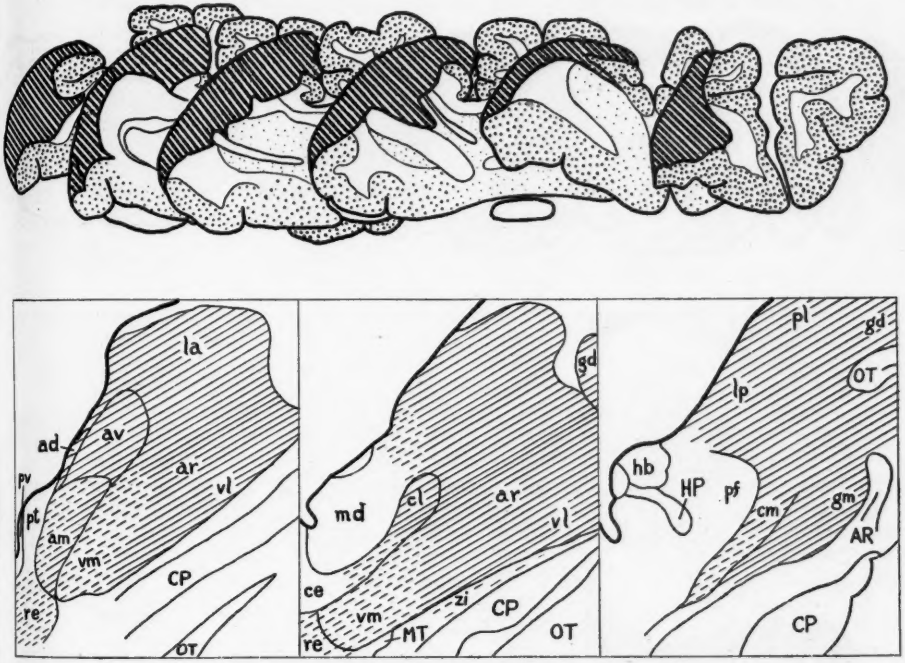

Fig. 1. Cat 97. A series of six drawings of sections (above) showing the extent of the lesion, and three sections (below) showing the degeneration in the thalamus. In the lesion drawings the stippling indicates normal tissue. In the drawings of the thalamus complete degeneration is indicated by parallel diagonal lines, and partial degeneration by diagonal broken lines. *CP*, cerebral peduncle; *OT*, optic tract; *MT*, mammillothalamic tract; *HP*, habenulopeduncular tract; *AR*, auditory radiation; *ce*, central nucleus; *hb*, habenular nucleus; *pv*, paraventricular nucleus; *pt*, parataenial nucleus; *zi*, zona incerta. Abbreviations for the other thalamic nuclei are given in Table I.

caudal part of the right cingulate gyrus was not completely removed. The rostral tip of the dorsal thalamus, including the enlarged rostral tip of the reticular nucleus, was destroyed, as was also all of the right hypothalamus rostral to the optic chiasma.

Cat 115. Almost the entire neocortex of the right hemisphere was removed, but the experiment was imperfect in that part of the corpus striatum was

destroyed. A narrow strip of gyrus cinguli remains on the right side, but practically all of its fibre connexions were severed. The ventral margin of the lesion lay along the rhinal fissure, leaving the hippocampal cortex for the most part normal. The inrolled hippocampus was injured superficially where it lies over the caudal half of the thalamus. There was a small wedge-shaped cut into the precrucial gyrus of the left side, shown in the first diagram (Fig. 3). More than half of the right caudate nucleus was removed, and the remainder is seen

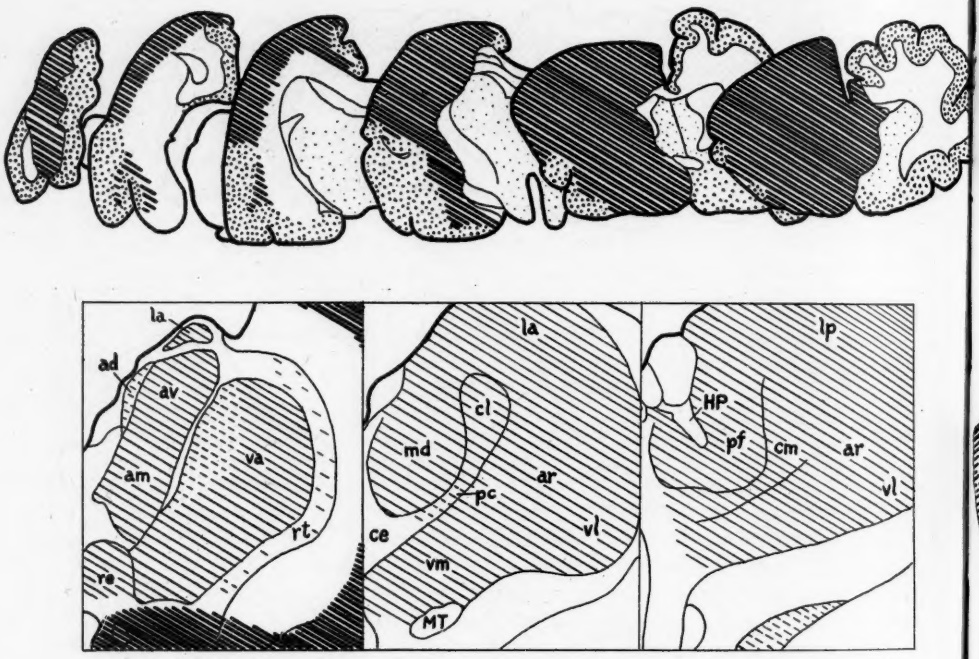

Fig. 2. Cat 98. Six drawings of sections to show the lesion, and three sections through the thalamus. In the lesion drawings and in the first of the thalamus drawings the heavy diagonal lines indicate tissue removed or destroyed at operation. As shown in the first thalamus drawing the lesion in the hypothalamus approached the ventral part of the dorsal thalamus.

in the sections to be distorted dorsally to such an extent that its limits are difficult to recognize. The lateral part of the lentiform nucleus was somewhat injured. The superficial surface of the occipital lobe was cut away, but part of the cortex of its deep surface was spared. The right side of the septum pellucidum, slightly injured by the lesion, was distorted dorsally along with the thalamus, which was also very slightly injured at operation.

Cat 120. The neocortex of the left side was almost completely removed, but unfortunately a large part of the corpus striatum was destroyed. A narrow strip of gyrus cinguli remains on the lesion side, and the under-surface of the

occipital lobe was not completely removed, but the frontal lobe and the tip of the occipital lobe were entirely cut away (Fig. 4). The lateral part of the hippocampal gyrus was destroyed, but the hippocampus itself remained largely intact. The lentiform nucleus was practically obliterated, and at least half the cells of the caudate nucleus were either directly destroyed by the lesion or included in a zone of dense infiltration of neuroglia. The head of the caudate nucleus was distorted dorsally so that its boundaries are difficult to recognize in the sections. A diagonal cut entered the left side of the septum pellucidum. Rostrally on the right side a small clot replaced part of the dorsomedial corner of the precrucial gyrus, and the medial surfaces of the cingulate and splenial

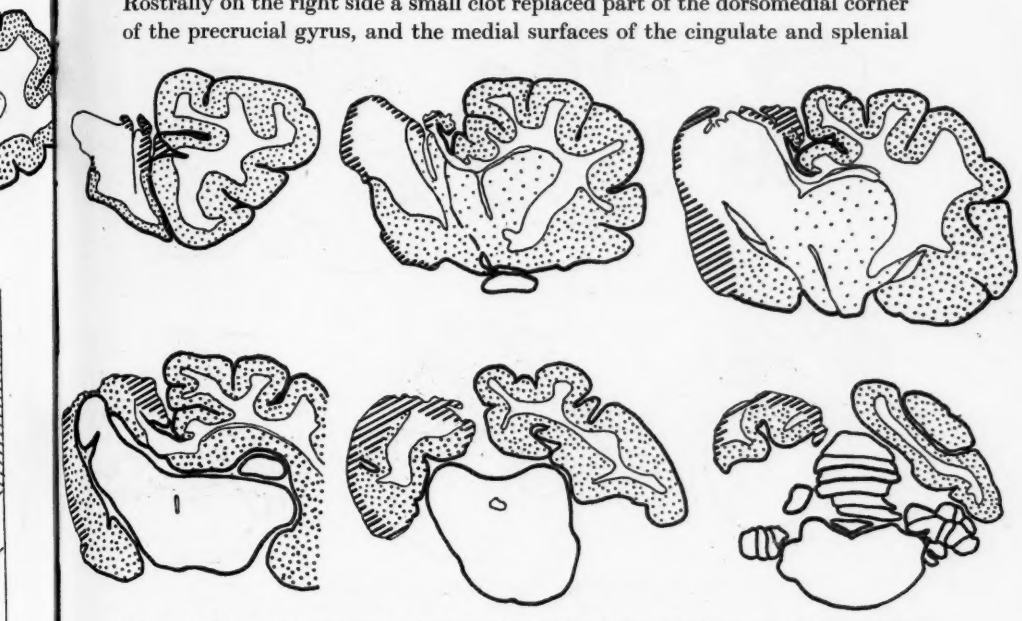

Fig. 3. Cat 115. Six drawings to show the extent of the lesion. The distortion of the caudate nucleus was such that its boundaries, in the section from which the second drawing was made, could not be definitely determined.

gyri were injured by compression. The rostral part of the left thalamus was somewhat distorted, as shown in the third section in the illustration, but there was no direct injury to the thalamus. Its caudal part, which is covered by the hippocampus, was not distorted.

DISCUSSION OF THALAMIC DEGENERATION

Serial sections of the brains of the four animals showed that in each case an extensive region of complete degeneration occupied the major part of the dorsal thalamus on the operated side. A general summary of the distribution of degeneration is given in Table I. No contralateral cell reaction was found,

in the thalamus or elsewhere, although there were several accidental injuries contralateral to the major lesions.

The *anterodorsal nucleus* was completely degenerated only in cat 97, in which there was a slight injury of the thalamus immediately lateral to the anterior tubercle. In each of the three other experiments some cells of *ad* remained well preserved, mainly in its caudal and ventral part. The existence of the ascending cortical fibres from the anterodorsal nucleus to the caudal part of the gyrus cinguli (Clark & Boggon, 1933) is thus confirmed, but there is

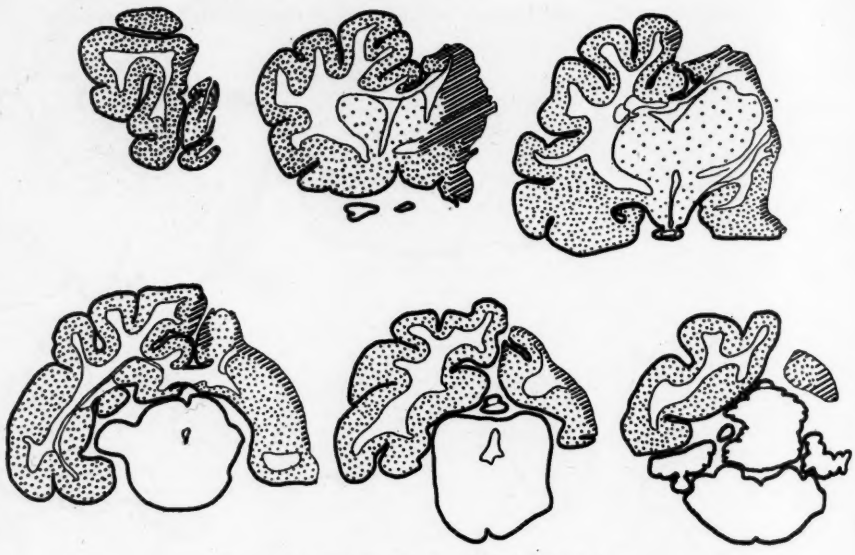

Fig. 4. Cat 120. Six drawings showing the lesion.

probably also a prominent subcortical efferent connexion arising in the cells which did not completely degenerate (Waller, 1934). Since the cingulate gyrus was not entirely destroyed in the present experiments, the possibility must be kept in mind that the cortical area receiving fibres from *ad* may not have been completely removed.

The *anteromedial nucleus*, which sends fibres to the rostral part of the gyrus cinguli (Waller, 1934; Walker, 1936), exhibited degeneration in its lateral half in cat 97, from which the frontal cortex was not removed; hence the ascending fibres from *am* must be distributed through at least the rostral half of the gyrus cinguli (Waller, 1937) rather than concentrated in a small frontal area as in the rat. In cats 97 and 115, in which the frontal lobe was well removed, the degeneration of *am* was practically complete, leaving only a very small group of cells medially. Because of extensive subcortical injury these results are not adequate to demonstrate the existence of any cortical

connexion for the medial part of the anteromedial nucleus, especially in view of the fact that Bard & Rioch (1937) found degeneration only in the lateral part of the nucleus after a very extensive cortical lesion (their animal no. 313). Moreover, in two unpublished experiments in which the writer removed large

Table. I. *Summary of lesions and degeneration.*

Lesion		Cat no. 97	98	115	120
Caudate nucleus		X	XXX	XX	XX
Lentiform nucleus		X	XXX	X	XXX
Septum pellucidum		.	XX	X	X
Hippocampus		X	X	X	X
Thalamus		X—	X	X—	.
Neocortex remaining		Front.	Occip.		
	Thalamic degeneration				
ad	anterodorsal	XXX	XXx	XXx	XXx
av	anteroventral	XXX	XXX	XXX	XXX
am	anteromedial	XX	XXx	XXx	XX
la	lateral anterior	XXx	XXx	XXx	XXx
lp	lateral posterior	XXX	XXX	XXX	XXX
pl	pulvinar	XXX	XXX	XXX	XXX
va	ventral anterior	XXx	XXx	XXx	Xxx
vm	ventromedial	X	XXX	XXX	XXX
vl	ventrolateral	XXX	XXX	XXX	XXX
ar	arcuate	XXX	XXX	XXX	XXX
rt	reticular	XX	X	XX	XX
re	reuniens	XX	XXX	XXX	XX
cl	central lateral	XX	XX	XX	XX
pc	paracentral	X	X	XX	XX
cm	centrum medianum	Xx	Xx	Xxx	Xx
md	medial	X	XXx	XXx	XX
gd	dorsal nucleus of lateral geniculate	XXX	XXX	XXX	XXX
gm	medial geniculate	XXX	XXX	XXX	XXX
pf	parafascicular	x	XXx	XX	XX
sm	medial nucleus of septum pellucidum	XX	XXX		

In the upper part of the table are shown the estimated amounts of operative injury to various parts of the brains, XXX denoting practically complete destruction. A single X indicates destruction of about one-third of a structure. Very slight injury to the thalamus in cats 97 and 115 is marked X—.

Chromatolytic reaction in the cells of the thalamic nuclei is shown in the lower part of the table, with its extent of distribution in each case indicated by the same signs. Thus XX denotes degeneration of about two-thirds of the cells in a nucleus. Partial degeneration of some cells is shown by a small x. Thus XXx denotes complete degeneration in two-thirds of the cells of a nucleus and partial degeneration of the remainder. Nuclear masses in which no cell reaction was found are not included in the table.

parts of the rostral half of the gyrus cinguli of the cat the anteromedial nucleus failed to degenerate completely. In one of these about four-fifths of the cells of *am* showed cell reaction, leaving the medial part of the nucleus normal.

The *lateral nucleus* showed cell changes in all of its parts. Some of the cells in the pars anterior (*la*) were not as markedly affected as most of the cells in the zones of complete degeneration. Clark & Boggon (1935) found no cell changes

in the lateral anterior nucleus after several lesions of the parietal cortex of the monkey, but were careful to avoid a definite statement that *la* has no cortical connexions. Their conclusion (p. 352) that "element *La* either has no cortical connexions with the frontal and parietal lobes at all, or, if they are present, they must be very few and scattered", is judicious, in view of the fact that their series did not include any very extensive lesions. Walker (1935) found degeneration of only part of the cells of *la*, and concludes (1936, p. 33) that this nucleus sends no fibres to the cortex. On the other hand, Bard & Rioch (1937, p. 83) found that following decortication the "lateral nucleus contained only fibres and glia besides a few pale, shadowy ganglion cells in the pars anterior". It may be argued that the decortication experiments which have shown lateral anterior nucleus degeneration were complicated by subcortical injury, but unmistakable degeneration of this nucleus has been seen in the rat (Waller, 1934) following limited cortical lesions with no subcortical involvement. Apparently the lateral nucleus pars anterior is connected to the cortex, but less strongly than some other thalamic nuclei.

The *ventral anterior nucleus* was included in the region of degeneration in each of the four experiments, but in three of them the medial part contained some normal or nearly normal cells. The region which only partly degenerated is indicated in Fig. 2. Degeneration of the ventral anterior nucleus has been found in the rat (Waller, 1934) and monkey (Clark & Boggon, 1935). In the cat (Waller & Barris, 1937) frontal lesions have caused cell changes in the lateral part of *va* but not in its medial part. Bard & Rioch (1937, p. 83) found the nucleus "almost completely degenerated, with only occasional ganglion cells remaining". The ventral anterior nucleus, like the lateral anterior, has, then, an ascending cortical connexion, but contains some cells, chiefly in its medial part, which have prominent subcortical efferent fibres.

The *ventromedial nucleus* degenerated completely in three of the experiments, but in cat 97, in which the frontal lobe was not removed, only part of its cells were affected. In sections of this brain the remaining normal cells are scattered evenly through the territory of *vm*, intermingled with degenerated cells. Such scattering degeneration is frequently caused by undercutting of the fibre connexions of a part of the cortex, and it is evident from the drawings of the lesion in cat 97 that many of the fibres of the frontal cortex were cut. The ventromedial nucleus (see Figs. 1 and 2) includes both the ventromedial and the submedial nuclei of Ingram *et al.* (1932) and of Papez & Aronson (1934). It is apparently equivalent to the ventral part of the ventral anteromedial nucleus of Clark & Boggon (1935), who found no cell reaction in this region. Bard & Rioch (1937) found some normal cells remaining after decortication in the medial part of the ventral nucleus of their cat 313. The ascending connexion from *vm* to the frontal cortex has been demonstrated in the rat (Waller, 1934). It was not found in previous experiments with the cat (Waller & Barris, 1937), probably because none of the lesions covered the proper part of the cortex.

The *reticular nucleus* (Fig. 2) contained a mixture of normal and degenerated

cells in the sections of each of the four brains. According to Bard & Rioch (1937) the reticular nucleus remained normal, except for accumulation of neuroglia cells, after decortication (their cat 313). Thus it appears that the reticular nucleus is not simply the "cortex" of the ventral thalamic nucleus, but is, rather, an independent structure with different efferent connexions, less intimately related to the cortex than is the ventral nucleus.

Nuclei of the midline. The results of the hemidecortication experiments are not thoroughly in agreement with the frequently reiterated statement that the midline nuclei have no ascending cortical connexions. There were no cell changes in the *parataenial*, *paraventricular*, or *central* nuclei, but in every case there was pronounced degeneration of the *nucleus reuniens*. Extensive subcortical injuries invalidate three of the experiments as evidence in themselves of the existence of a cortical connexion from this cell group, but in cat 97, which had very little subcortical involvement, there is indication that it may send some fibres to the cortex. The result of one experiment cannot, of course, be accepted as proof without confirmation. The degeneration in cat 97 was of the scattering type, normal cells being mixed with degenerated ones in the sections. About two-thirds of the cells of the nucleus degenerated, and the contrast between the nucleus reuniens of the operated side and the normal one immediately adjacent to it across the midline is striking.

The *medial nucleus* was only slightly degenerated in its lateral part in cat 97, in which the frontal cortex was not removed, and it is likely that this degeneration was caused by undercutting rather than by removal of cortical tissue. In cat 120 the degeneration was more extensive, but still in the lateral two-thirds of the nucleus. The more nearly complete degeneration in cats 98 and 115 was probably caused in part by subcortical injury, since experiments with the monkey (Clark & Boggon, 1935; Walker, 1936) indicate that the medial part of the medial nucleus is not connected to the cortex. The results of earlier experiments with the cat were interpreted (Waller & Barris, 1937) as evidence that the connexion of the medial nucleus is to the gyrus proreus, but more recent results (to be published) seem to show that medial nucleus fibres go to cortex lateral rather than medial to the presylvian sulcus.

The *central lateral* and *paracentral nuclei* exhibited varying degrees of cellular degeneration, usually of the scattering type, in all four experiments (Table I). In no case were all the cells of either of these nuclei affected. In cat 97, which was the best of the experiments because the subcortical injury was slight, the medial part of the paracentral nucleus, which lies next to the normal central nucleus, retained the majority of its cells intact. The results for the intralaminar nuclei are in general agreement with those of Bard & Rioch (1937, p. 83), who found the paracentral nucleus partly, and the central lateral nucleus completely, degenerated. It has not been customary to describe cortical connexions for the intralaminar nuclei, and it is probably true that some of the cells of these groups have no ascending cortical fibres. Some of the degeneration found in the present experiments and in those of Bard & Rioch

may have been caused by subcortical injury, but cell reaction following cortical injury without subcortical involvement has previously been found in the central lateral nucleus of the rat (Waller, 1934) and in the paracentral nucleus of the cat (Waller & Barris, 1937). It is therefore reasonable to conclude that some of the cells in each of these nuclei have ascending cortical connexions.

The *centrum medianum* has been differently identified by several writers in recent years. It was described by Ingram *et al.* (1932) as a region containing widely scattered cells, lying medial to the arcuate nucleus. In the rat a similarly situated, although larger, region containing small cells quite widely scattered, was identified as centrum medianum by the writer; cell reaction after cortical lesions having demonstrated the existence of ascending cortical connexions, an area *cm*, in which the fibres end, was outlined on the cerebral cortex (Waller, 1934). The corresponding region in the cat (somewhat larger than the centrum medianum of Ingram *et al.*) consists of scattered cells lying ventrolateral to the medial and parafascicular nuclei, and was the site of cell reaction in one previous experiment (Waller & Barris, 1937). In three of the hemidecortication experiments scattered degeneration was found in this region, and in the other (cat 115) all the cells were affected. Thus there can be no doubt that the zone of scattered cells between the medial and parafascicular nuclei medially and the arcuate nucleus laterally gives rise to ascending cortical fibres. There is, however, a question concerning the identity of this region with the centrum medianum of human anatomy. The most recent authoritative discussion of the centrum medianum (Papez & Rundles, 1937) identifies it as a group of densely packed cells continuous with the ventral part of the parafascicular nucleus, and subscribes to the conclusion of Clark & Boggon (1935) that it has no ascending cortical connexion. In the present paper, as well as in previous ones, the writer includes this group of densely packed cells as a part of the parafascicular nucleus, which will be discussed below. The centrum medianum of Sager (1933), who found a cortical connexion, is probably this group of densely packed cells.

The *parafascicular nucleus* was completely degenerated in cat 98, in which the lesion destroyed the rostral part of the hypothalamus. Degeneration of some cells, mainly in its lateral part, in cats 115 and 120, must for the present be interpreted as due to subcortical injury, since in no previous cortical lesion experiments have cell reactions been found in *pf*. However, a few cells in the ventral part seem to have been somewhat affected in cat 97. As explained above, the ventral part of the parafascicular nucleus includes the group of densely packed cells which is called by some leading authorities the centrum medianum. It is precisely in this group that the doubtful cell reactions occurred, but there was not sufficient evidence to establish the existence of thalamocortical fibres arising here. Further experiments will be required to confirm the result of the experiment with cat 98, which indicates that fibres from the parafascicular nucleus go to some part of the hypothalamus.

The *ventral nucleus of the lateral geniculate body* was in a doubtful state of

preservation in cats 115 and 120. Although most of its cells were certainly normal, it is possible that a few may have been slightly affected by the lesions. The change was not sufficiently definite to be classed as degeneration.

The *septum pellucidum* was the site of a striking reaction in cats 97 and 98. In the former there was partial, and in the latter complete, degeneration of the medial large-cell nucleus (nuc. parolfactorius medianus of Johnston, 1913). In cat 98 the thin rostral part of the septum was completely destroyed on both sides. Since the medial large-cell nucleus on the left side was not affected, it is evident that the degeneration on the right side was not caused by injury to fibres passing rostrally in the septum. There was some injury to the hippocampus in both experiments, but the main body of the fornix was not injured in cat 97. Since the large cortical lesions in cats 115 and 120 failed to produce recognizable cell reaction in the septum, it cannot be definitely stated that the degeneration in the two other experiments was caused by cortical injury.

CONCLUSIONS

The value of the present series of hemidecortication experiments is somewhat lessened by the accidental injuries of subcortical structures at operation, as has been mentioned. Failure to find complete degeneration in a thalamic nucleus, as in the reticular nucleus, is excellent proof that its cells do not send their efferent fibres exclusively to the cortex, but less confidence can be placed in the positive findings for the ventromedial, lateral anterior, paracentral and central lateral nuclei, which are thought by some writers to have no ascending cortical connexions. The possible destinations for efferent fibres from these thalamic nuclei are, however, limited. Present knowledge of the thalamus could hardly justify the assumption of any very highly developed subcortical efferent connexions other than to the corpus striatum or to other thalamic nuclei. In an effort to find evidence of the existence of thalamo-striate connexions the writer has made a considerable series of lesions in various parts of the corpus striatum of the cat with the Horsley-Clarke stereotaxic apparatus, and has found it exceedingly difficult to obtain cell reaction in the dorsal thalamus. Although this work is yet incomplete, it appears that we shall be forced to look elsewhere for the efferent connexions of most of the thalamic cells which do not degenerate after cortical lesions. And if the corpus striatum is relatively unimportant as a receptive organ for stimuli from the thalamus, the hemidecortication experiments, crude as they are, may still be quite dependable, since the subcortical involvement which is thought to vitiate their results consists chiefly of striatal injury. If the subcortical efferent connexions of the thalamic nuclei are mainly intrathalamic, they were certainly not involved in the present group of experiments.

The principal nuclear groups in the dorsal thalamus, such as the ventrolateral nucleus, which have well-proved ascending cortical connexions, probably have also, as mentioned above, numerous short fibres connecting to neighbouring thalamic nuclei. Since all of the cells of the ventrolateral nucleus,

for example, exhibit profound cell reaction following properly placed cortical lesions, it appears that a single thalamic cell may have axon branches going to two or more parts of the brain. Pronounced degeneration of a thalamic cell after cortical lesion demonstrates the great importance of the cortical axon branch in the life and activity of the cell. Chromatolytic reaction of lesser degree in some of the cells of a nucleus, as described above in the lateral anterior nucleus, indicates that the cortical axon branches of these cells are relatively less important, and that they normally devote a greater part of their energy to sending nerve impulses over subcortical efferent axones. Although it is possible that partial degeneration may occur in a thalamic cell as a result of degeneration of other cells in the thalamus to which it is connected by intrathalamic fibres, it would be unreasonable, with the crude methods of study now available, to interpret all partial degenerations as transneural atrophy. The extent of cell reaction following cortical lesion, then, may be used as a measure of the relative importance of the ascending cortical connexion in the activity of the cell.

According to the extent to which they are affected by cortical lesions, the nuclei of the dorsal thalamus may be classified into four groups. The first consists of the anteroventral, ventrolateral, ventromedial, arcuate and lateral posterior nuclei, the pulvinar, the medial geniculate body, and the dorsal nucleus of the lateral geniculate body, all the cells of which show pronounced reaction and are therefore strongly connected to the cortex. In the second group are the nuclei which contain some cells that do not completely degenerate, and may be said to have cortical connexions of relatively less importance. These are the lateral anterior, anterodorsal, ventral anterior, central lateral and reticular nuclei, and the group of scattered cells identified as the centrum medianum. The first and third of these (*la* and *va*) are more intimately related to the cortex than are the others. Group three comprises the medial, anteromedial and paracentral nuclei, the medial part of each of which is composed of cells which have not been shown to have any ascending cortical connexion. Finally the fourth group, composed of the parafascicular, parataenial, paraventricular, and central nuclei, and the ventral nucleus of the lateral geniculate body, has, so far as we are at present aware, no ascending cortical connexions at all. Probably the nucleus reuniens should for the present be included in group four.

SUMMARY

In four cases of nearly complete hemidecortication in the cat, with varying amounts of injury to subcortical structures, complete degeneration was found in the anteroventral, ventromedial, ventrolateral, arcuate and lateral posterior nuclei, the pulvinar and the geniculate bodies. Nearly complete degeneration of the lateral anterior and ventral anterior nuclei, and partial degeneration of the anterodorsal, anteromedial, reticular, medial, paracentral and central lateral nuclei, and the centrum medianum, indicates that these nuclei have

cortical connexions in addition to well-developed subcortical efferent fibres. Cell reactions found in the nucleus reuniens and the medial large-cell nucleus of the septum pellucidum are not necessarily to be interpreted as evidence of cortical connexion because of the involvement of subcortical structures in the lesions. Complete degeneration of the parafascicular nucleus in one case was probably caused by injury to the hypothalamus. No cell changes were found in the parataenial, paraventricular, or central nuclei, or in the group of nuclei about the posterior commissure, nor was there any definite degeneration in the ventral nucleus of the lateral geniculate body.

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THE CONNEXIONS OF THE POSTERIOR COMMISSURE

A STUDY OF ITS DEVELOPMENT AND MYELINATION IN THE HUMAN FOETUS AND YOUNG INFANT, OF ITS PHYLOGENETIC DEVELOPMENT, AND OF DEGENERATIVE CHANGES RESULTING FROM CERTAIN EXPERIMENTAL LESIONS

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INTRODUCTION

During an investigation (Keene & Hewer, 1933) of the development and connexions of the medial longitudinal bundle in the human, the posterior commissure was brought frequently to our notice, and we were impressed not only by the early date at which it may be detected in the human embryo, but also by the early definition of its pattern during development. The latter suggests that this commissure possesses very constant connexions but, on referring to the literature on the subject, it was found that except for one generally accepted connexion (the nucleus of the posterior commissure, also known as the nucleus of Darkschewitsch), other connexions were often vaguely described and varied greatly according to different authors. A further investigation of this region was therefore undertaken, and the scope of the proposed research was designed to include a study of the development, myelination and connexions of the commissure in the human, and also a review of its phylogenetic development.

However, when this work was nearly complete, it was recognized that though a study of the onset of myelination of the fibres of the commissure in a large series of human foetuses affords a means of differentiating between the fibres, and defines certain connexions, yet it yields very little information as to the precise disposition of its component neurones. Prof. W. E. Le Gros Clark suggested that examination of degenerated fibres following section of the commissure would throw light on this point, and also kindly offered to perform the experiment. The work therefore includes some observations on the results of certain experimental lesions.

MATERIAL

The material on which this paper is based includes serial sections of brains of forty-four human specimens, and serial sections of brains of twenty-one specimens of vertebrate animals.

The following list gives the method of staining of the material, and in the case of human material gives the age.

Human material

Age	No. of specimens	Staining	Age	No. of specimens	Staining
*9 mm.	2	H. and B.S.	80 mm.	2	R.
*10 mm.	2	H. and B.S.	80 mm.	1	H. and B.S.
*12 mm.	3	H. and B.S.	*14–16 week foetus	1	W.P.
*12·5 mm.	1	H. and B.S.	15 week foetus	1	R.
*16 mm.	1	R.	16–18 week foetus	1	Bielschowsky
*17 mm.	1	H. and B.S.	18 week foetus	1	R.
*18 mm.	2	H. and B.S.	*24 week foetus	1	R.
*19 mm.	2	H. and B.S.	24–26 week foetus	2	W.P.
*20 mm.	1	H. and B.S.	26–28 week foetus	1	H. and B.S.
*25 mm.	1	H. and B.S.	36 week foetus	1	W.P.
*32 mm.	1	H. and B.S.	Full-time foetus	2	W.P.
8 weeks	2	H. and B.S.	3 day infant	1	W.P.
37 mm.	1	H. and B.S.	*3 month infant	2	W.P.
10 weeks	1	H. and B.S.	6 month infant	1	W.P.
67 mm.	1	R.	7 month infant	1	W.P.
75 mm.	1	Picrocarmine	8 month infant	1	W.P.
76 mm.	1	H. and B.S.	9 month infant	1	W.P.

Vertebrate animal material

Specimen	Number	Staining	Specimen	Number	Staining
**Petromyzon*	1	H. and B.S.	Salamander	1	H. and B.S.
*Skate	2	H. and B.S.	Chameleon	1	H. and B.S.
*Dogfish	1	H. and B.S.	Mole	1	W.P.
**Necturus*	3	H. and B.S.	*Kitten	1	W.P.
Necturus	1	R.	Cat	1	Osmic
Frog	2	H. and B.S.	Monkey	3	Osmic
Sphenodon	2	Ranson			

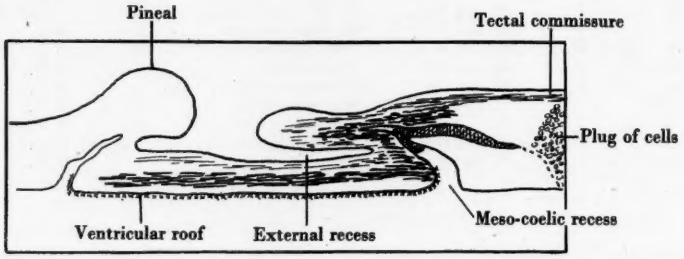
Note. H. and B.S. = Scott's haematoxylin and Biebrich Scarlet.
W.P. = Weigert-Pal's method.
R. = Ranson's method modified by Hewer (1933).
* denotes serial every section.

THE POSTERIOR COMMISSURE IN MAN

(*a*) *Position and general arrangement of the fibres within the tract*

The posterior commissure extends from the region of the pineal recess to the tectal commissure. Its caudal end corresponds with the position of the orifice of the mesocoelic recess (which closes soon after birth), and in the foetus the epithelial roof cells related to the commissure form the subcommissural organ. The plan of the developing commissure can be followed by reference to Text-fig. 1, which is a rough linear reconstruction of the tract in a 3-day infant. It is seen that the component fibres are of two kinds, coarse and fine. The coarse fibres lie close to the ventricular roof and also skirt the mesocoelic recess, whereas the fine ones occupy a position nearer to the exterior, and are continued into the tectal commissure. The curious fold of the roof of the mesencephalon in the cephalad direction which includes the mesocoelic recess occurs very early in embryonic life and is well seen in a 32 mm. embryo, but, as noted

in a previous paper (Keene & Hewer, 1935), it tends to disappear together with the mesocoelic recess 3 or 4 months after birth. The arrangement of the coarse and fine fibres of the commissure, however, remains undisturbed in spite of the disappearance of the fold. In fact the arrangement of the fibres in the caudal part of the commissure is such as one would expect if the external recess had become occluded by adhesion of its surfaces. Thus the cephalic part of the commissure consists of ventral coarse fibres and fine dorsal ones, and the caudal part (i.e. that part which in the foetus was related to the mesocoelic recess) has a more complicated arrangement of fibres, due to the forward folding of the roof of the mid-brain in that region.



Text-fig. 1. Linear reconstruction showing arrangement of coarse and fine fibres in the posterior commissure. (From 3-day infant.) ×××× denotes position of subcommissural organ.

(*b*) *Development and myelination*

Sections of human embryos of 9 and 10 mm. were examined, and in these the commissure was not identified but, in the 12 mm. embryo of this series, a large posterior commissure is present. The fact that the tract is so well developed in the 12 mm. embryo suggests that it must have been present though unrecognized in the younger specimens. Frazer (1931) states that it develops early in the second month.

The 12 mm. embryo exhibits a commissure formed chiefly of rather coarse fibres which may be traced ventrally, but no nucleus was identified. Some fibres connect with the subcommissural organ, others with the thalamus and tegmental region Embryos of 25–37 mm. (about 7–8 weeks) present a very well-developed commissure, and fibres still connect with the cells of the subcommissural organ.

About the 14th week myelination begins, and proceeds to develop in the various fibres in the following order:

(1) At the 14th week a few myelinated fibres are found in the ventral part of the commissure, and also in the nucleus chiefly connected with this group of fibres, the nucleus of the posterior commissure.

(2) At about the 24th week myelination is found in the fibres connecting with the subcommissural organ: and at this time the medial longitudinal

bundle shows a myelinated connexion with the nucleus of the posterior commissure, and also with the nucleus of the third cranial nerve.

(3) At the 36th week there are present delicate myelinated connexions with the medial habenular nucleus, with the habenulo-peduncular tract and with the pineal gland (Pl. I, fig. 5); and myelination is found in fibres connecting with the tegmentum and the red nucleus.

(4) At 3 months after birth the thalamic connexions are myelinated, and at about the same time myelination appears in some horizontal laterally directed fibres.

The myelination of each group is at first very fine and increases later, particularly with regard to the ventral group.

The connexion with the subcommissural organ is curious. It is large and unmyelinated at 8 weeks, at 24 weeks it appears to be diminished though a few myelinated fibres are seen, and later on in foetal life the whole connexion disappears. In a previous paper the atrophy of the subcommissural organ in man has been noted (Keene & Hewer, 1935).

(*c*) *Connexions*

A very careful study of the development and myelination of the commissure in human specimens up to 9 months after birth permits the following summary of its connexions:

(1) The main bulk of the coarse fibres in the commissure connect with the nucleus of the posterior commissure (nucleus of Darkschewitsch of some observers) and also indirectly through the nucleus of the posterior commissure or interstitial nucleus with the ipsilateral medial longitudinal bundle (Pl. I, fig. 2).

(2) Other fibres, chiefly coarse ones, connect with the regions of the tegmentum and the capsule of the red nucleus (Pl. I, fig. 1).

(3) Fine fibres situated in the dorsal part of the commissure connect with the thalamus (Pl. I, fig. 3).

(4) There is a well-marked component of the commissure consisting of horizontal fibres which may be traced in a lateral direction. After repeated examination of the sections it was thought that this connexion may be striatal, or possibly cortical (Pl. I, fig. 4).

(5) There is a small connexion with the habenular ganglia, and the habenulo-peduncular tracts (Pl. I, fig. 5).

(6) A fine connexion with the pineal gland is also established.

THE PHYLOGENY OF THE POSTERIOR COMMISSURE

Petromyzon (Pl. II, fig. 1)

The posterior commissure of petromyzon and other myxinoids has been well described by several observers (Johnston, 1907; Herrick, 1913; Jansen, 1929; Schilling, 1907; Kappers, 1936). It consists of a commissural mass of fibres

related to the caudal part of the subcommissural organ, and both structures end abruptly at the opening into the recess of the mid-brain. A marked connexion exists between the commissure and the subcommissural organ, but the cells of this organ also connect with many fibres which lie in the commissural mass but which do not cross.

The nucleus of the posterior commissure is not identified in our specimens. Most of the fibres spread ventrally amongst some scattered cells, and then are lost among the other fibre tracts. Jansen (1930), having examined 200 myxine brains, could not identify a nucleus of the posterior commissure.

The tectal component described by Johnston and Tretjakoff (Tretjakoff, 1909) was not seen by us, and the posterior commissure is separated from the tectum by an extensive evagination of the epithelial roof of the mid-brain.

Skate and dogfish

The brains of skate (Pl. II, fig. 2) and dogfish show a very large posterior commissure, exhibiting a great advance on that of petromyzon, and corresponding very closely in form and extent with the human type. The nucleus of the posterior commissure was not identified, but the coarse ventral fibres in the commissure correspond very closely to those which in the human are derived from this nucleus. Other fibres appear to connect (as in the human) with the diencephalon and the tegmentum. Some spread in a lateral direction, possibly representing the external geniculate connexion mentioned by Kappers (1936). There is a well-marked connexion with the subcommissural organ.

Necturus

The posterior commissure in *Necturus* is much simpler in form than that of skate or dogfish.

It is related dorsally to the commissura tecti diencephali which overlaps the posterior commissure both cephalically and caudally. The subcommissural organ is very large and lines the roof of the aqueduct as high up as the habenular commissure and extends below the caudal range of the posterior commissure. The chief connexion of the commissure apart from that with the subcommissural organ, appears to lie with cells of the grey matter in the ventral region of the brain stem, probably the nucleus tuberculum posterius of Herrick (1928).

It was felt that the selection of necturus for exhibiting the amphibian type of the posterior commissure was not doing justice to that order, and the brain of a frog was next examined.

Frog

The posterior commissure is well developed, and exhibits most of the features described in the human, including the coincidence of the position of the orifice of the mesocoelic recess with the lower limit both of the com-

missure, and of the subcommissural organ. The bulk of the ventral fibres of the commissure connect with cells situated close to the upper limit of the nucleus of the third nerve and the medial longitudinal bundle. It is difficult to differentiate a definite nucleus in this situation, but the position of these cells corresponds very closely to that of the nucleus of the posterior commissure in the human. The commissure exhibits a marked connexion with the subcommissural organ.

The commissure differs from the human in that it does not extend up to the pineal recess, and also that a large bulk of the dorsal group of its fibres connect with the optic lobes.

Salamander (Pl. II, fig. 3)

The posterior commissure is relatively simple, consisting mainly of coarse fibres which, when traced ventrally and caudally, lose their identity by mingling with other fibre tracts in close relation with the third nerve nucleus.

There are, however, in addition to this ventral bundle, a few fine fibres passing dorsal to a small mesocoelic recess which correspond to the dorsal component of the commissure found in skate and frog. There is a marked connexion in the cephalic part with the cells of the subcommissural organ.

Chameleon

The commissure in this reptile follows very closely the human plan. The coarse ventral fibres are derived very largely from a nucleus situated in close relation to the nucleus rotundus. Traced from the commissure in a caudal direction, these fibres continue for some distance in the ventral part of the brain stem and lose their identity when in close relation to the third nerve nucleus, by mingling with other coarse fibre bundles. The components of the dorsal group of fibres of the commissure connect with the tectum and with the ventrolateral region of the brain stem. The ventral fibres of the commissure connect freely with the subcommissural organ.

Sphenodon[1]

The commissure is well developed and differs only in certain respects from the human type. The mesocoelic recess is absent in the two specimens examined.[2] There is a very well-marked connexion with the subcommissural organ and with the optic lobes.

The coarse ventral fibres of the commissure connect with ventrally placed cells of the grey matter in the mid-brain, but no nucleus of the posterior com-

[1] Kindly lent by the late Dr McMaster.

[2] It must be remembered however in regard to the presence or absence of this recess that in comparing the series of animals with the human series a comparison is being drawn between post-natal, often adult, material on one hand with foetal or very young post-natal material on the other.

missure is defined. Compared with chameleon, the cephalic end of the commissure exhibits a marked difference in that it effects a delicate connexion with epiphyseal structures and with the habenular ganglia.

Mole (Pl. II, fig. 4)[1]

The commissure in the mole consists of very heavily myelinated fibres occupying chiefly the ventral part of the commissure, though some of these fibres pass into the dorsal part. They connect on either side with the nuclei of the posterior commissure, and appear to arise from cells of this nucleus. Other heavily myelinated fibres lying in the ventral part connect with the tegmental region. In addition to the coarse fibres mentioned above, there are also fine myelinated fibres in the dorsal part of the commissure which are directed laterally and horizontally. This dorsal part of the commissure is confluent with the tectal commissure. A well-developed subcommissural organ is present, and a mesocoelic recess is also seen. The commissure thus very closely resembles that in the human.

In mole and in the kitten examined (Pl. III, fig. 1), there is found in addition a well-marked bilateral nucleus lying rather dorsally placed among the fibres approaching the commissure. This nucleus is also figured by Rioch (1929) in his studies on the diencephalon of carnivora, and called by him the "nucleus of the posterior commissure", but it does not give rise to a great many fibres entering the commissure; it must not be confused with the large nucleus lying more ventrally in close relation with the red nucleus and nuclei of the third nerve, which does furnish abundant fibres to the commissure, and which he calls the nucleus of Darkschewitsch, and which corresponds to the one described in this paper as the nucleus of the posterior commissure. Attention has already been drawn in another paper (Keene & Hewer, 1933) to the great confusion that reigns regarding these nuclei. This confusion is probably due to the fact that the dorsally placed nucleus consists of only a few cells in the human, whereas in the lower mammals that we have examined (cat, mole) it is certainly a well-marked collection of cells, though not so important to the commissure as regards fibre connexions, as the more ventrally placed nucleus.

Kitten (3 *weeks*) (Pl. III, figs. 1, 2)

In this specimen stained by the Weigert-Pal method, the commissure is seen to conform closely to that in the newborn infant. The ventral fibres of the commissure are well myelinated and consist chiefly of fibres connected with the nucleus of the posterior commissure, and also with a nucleus (Pl. III, fig. 1) situated dorsally, actually lying among the fibres approaching the commissure. Tegmental fibres also join the ventral part of the commissure. In the dorsal part are finely myelinated fibres which enter the commissure from a lateral direction. No connexion is seen with the subcommissural organ, which is well

[1] Kindly lent by Dr Una Fielding.

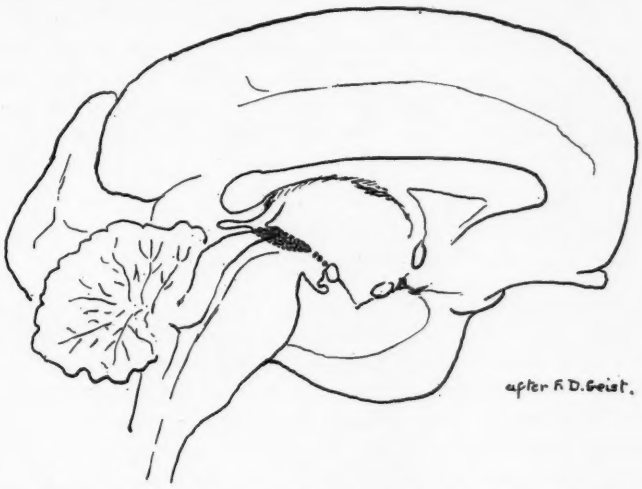
developed in the region of the commissure. A mesocoelic recess is not present in the specimen examined, possibly its presence post-natally varies as it does in man, for it has been observed in the adult cat. The medial longitudinal bundle is well myelinated and its cephalic fibres appear to connect with cells, probably belonging both to the nucleus of the posterior commissure and to the interstitial nucleus (Pl. III, fig. 2).

OBSERVATIONS ON EXPERIMENTAL MATERIAL

Operation

Rhesus monkey (O.M. 45) operated[1] 4 June 1936, killed 18 June 1936.

The operation was undertaken with the object of cutting through the posterior commissure, the animal being under nembutal anaesthesia.



Text-fig. 2. Diagram of brain of *Rhesus* monkey to show position of lesion.

The brain was exposed by raising an osteoplastic flap, and, approach being made from the left side, the left occipital lobe was drawn laterally and section of the commissure was made with a knife. The animal made a good recovery, and suffered no apparent disability, though no special tests were carried out. After fourteen days the animal was killed by an overdose of chloroform; the brain was removed and serial sections were stained by the Marchi method.

The lesion (Text-fig. 2) was found to cut the commissure just to the left of the median plane. In the cephalic direction it involved the habenular region and here extended near to the ventral surface of the brain in the mammillary region. In the region of the commissure it extended through the grey matter

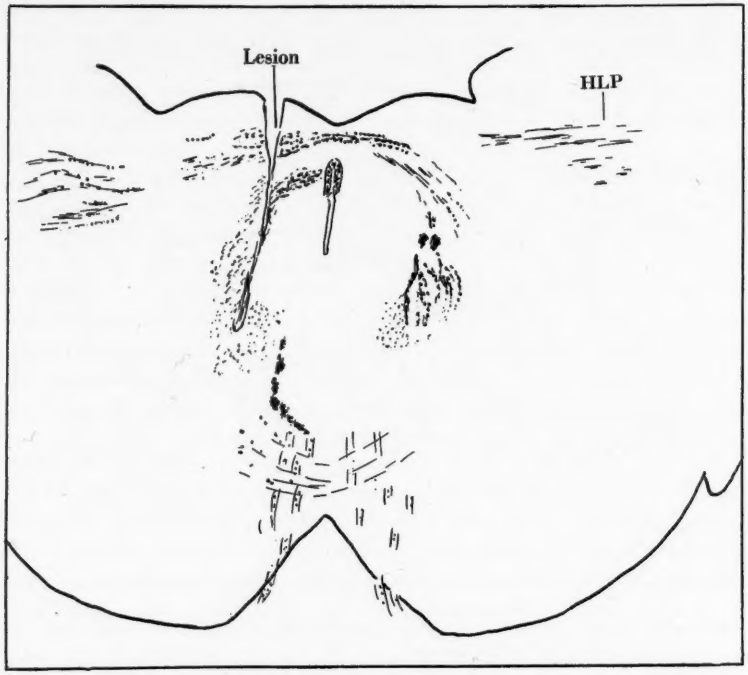
[1] The operation was performed at the Anatomical Department, University Museum, Oxford, by Prof. W. E. Le Gros Clark, M. F. L. K. assisting.

of the mid-brain, seriously damaging the nucleus of the posterior commissure and the interstitial nucleus, and caused some damage to the red nucleus and possibly very slightly affected the third nerve nucleus.

Caudally the cut was shallower and just impinged on the tectal commissure.

Degenerative changes

As may be seen from Text-fig. 3, degenerated fibres pass into both ventral and dorsal parts of the commissure, and these fibres may be traced into the



Text-fig. 3. Diagram showing lesion in monkey (O.M. 145). Degenerated fibres are dotted in.

HLP = horizontal laterally placed group of fibres.

regions of the opposite commissural nuclei (nucleus of the posterior commissure and interstitial nucleus) to the red nucleus and towards the tegmentum. The cephalic fasciculi of the ipsilateral medial longitudinal bundle are almost entirely degenerated and when traced caudally (Pl. III, fig. 3) these degenerated fibres are seen to occupy for the most part the medial part of the bundle.

Slight degeneration is found as follows:

(*a*) In ipsilateral horizontal laterally placed fibres (Text-fig. 3).

(*b*) In fibres of the third nerves, more marked on the side of the lesion.

(*c*) In a very few fibres of the contralateral medial longitudinal bundle.

Other degeneration found but not germane to this investigation was in the rubro-spinal decussation, in the habenular commissure, in the ipsilateral habenulo-peduncular tract, and further the contralateral habenular nucleus and habenulo-peduncular tract were also very slightly affected.

We were further indebted to Prof. Le Gros Clark for the loan of serial sections of experimental material in which the lesions which were designed for other investigations produced degeneration in fibres of the commissure. The evidence afforded by these sections relating to the posterior commissure is briefly noted.

In one specimen (cat 7) the lesion involved the right nucleus of the posterior commissure and in addition to finding the principal degeneration in the ventral part of the commissure, very definite degeneration was seen in fibres connecting with the contralateral thalamus.

In another specimen (monkey 46A) the nucleus of the posterior commissure was undamaged and the ipsilateral medial longitudinal bundle was found to be intact.

DEDUCTIONS BASED ON THE EVIDENCE OFFERED BY ALL PARTS OF THIS INVESTIGATION

(*a*) Efferent fibres arise in the nucleus of the posterior commissure of one side and pass to the nucleus of the commissure and interstitial nucleus of the other side, also to the contralateral red nucleus and tegmental region.

(*b*) The fibres shown to be degenerated passing from the nucleus of the posterior commissure to the opposite tegmentum do not appear sufficient in number to account for the large tegmental component of the commissure part of which must therefore be composed of fibres passing from the tegmentum to the commissure. It is suggested that these tegmental fibres may represent the secondary ascending vestibular tracts (Text-fig. 4), which have left the lateral part of the medial longitudinal bundle lower down.

(*c*) The cephalic part of the medial longitudinal bundle is almost entirely composed of descending fibres arising in the nucleus of the posterior commissure and interstitial nucleus, and lower down these fibres occupy chiefly the medial part of the bundle.

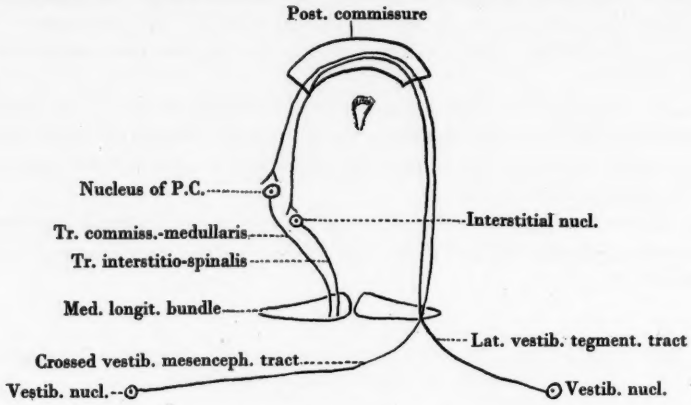
(*d*) Very few fibres which have crossed in the commissure pass directly into the medial longitudinal bundle.

(*e*) The degenerated fibres found among the horizontal laterally placed groups of fibres must be derived from ipsilateral cells, otherwise there would be degeneration in corresponding fibres on the other side.

(*f*) As there is practically no degeneration in the fibres of the horizontal

laterally placed group on the side opposite the lesion, it follows that these fibres must be still in relation with their cells of origin, and possibly indicates the presence of some descending fibres amongst this group (e.g. thalamo-commissural, striato-commissural, or perhaps cortico-commissural).

(*g*) The connexions that have been established show that the posterior commissure is of the nature of a decussation rather than a commissure. The only true commissural fibres appear to be those connecting the commissural nuclei (i.e. nuclei of the posterior commissure, and interstitial nuclei, and, in Carnivora, the dorsally placed nuclei of the posterior commissure of Rioch).



Text-fig. 4. Diagram illustrating connexions of secondary ascending vestibular tracts as described by Muskens.

(*h*) The chief connexions of the posterior commissure consist of the following groups of fibres:

(1) A ventral group present throughout the series, consisting of coarse fibres which in mammals connect with the nuclei of the commissure.

(2) Coarse fibres which connect with the tegmental region.

(3) Fine horizontal laterally placed fibres, possibly providing a striatal connexion.

(4) Fine fibres connecting with the thalamus.

(5) Fibres connecting with the tectum, found only in chameleon and in frog.

DISCUSSION

With respect to the bearing that the findings in this investigation have on the work of other observers, there is evidence offering confirmation for Muskens' (1922, 1935) conclusion that the secondary ascending vestibular tracts (the crossed vestibular mesencephalic, and the lateral vestibular tegmental) cross in the commissure before connecting with the nucleus of the posterior commissure, and the interstitial nucleus. They further confirm his experiment

which showed that the commissuro-medullaris, and interstitio-spinalis tracts (Text-fig. 4) are conducting in a downward direction, and occupy at lower levels the medial part of the medial longitudinal bundle. As already noted, we go further and offer evidence that these tracts form the most cephalic portion of the medial longitudinal bundle.

The degeneration in some of the horizontal laterally placed fibres indicates their ascending course and would support Muskens' suggestion that there are fibres passing from the commissural nuclei to the ipsilateral globus pallidus.

It has been noted that our sections show some degeneration in the red nucleus opposite to the lesion. Vogt (1919) and Riese (1924) observe some fibres which pass from the globus pallidus to the contralateral red nucleus. We in common with other workers can only note this commissuro-rubral connexion, but have no definite evidence as to the source of the fibres.

Table I

	Petromyzon	Skate	*Necturus*	Salamander	Chameleon	Mole	Kitten
Groups of fibres of commissure referred to on p. 498	**1**	**1234**	**1** ? 2	**1** ? 2	125	**123**	**1234**

Table showing composition of the posterior commissure in certain of the vertebrates studied. The numbers refer to the analysis of groups of fibres in § (*h*), p. 498. The figures in heavy type denote the groups furnishing the bulk of the fibres in each case.

With regard to any deductions that may be drawn from the phylogenetic study, it is recognized that this survey of the phylogeny of the commissure is very limited, and therefore any deductions from this part of the investigation are very tentatively made. It appears however fair to assume from the appearances of the tract in the various animals examined that the ventral part of the commissure is phylogenetically the oldest (Table I).

As to any information regarding functions of the commissure that may be suggested by the phylogenetic review, it is appreciated that the ground for argument is very uncertain. Several workers (Collier, 1927; Muskens, 1935; Duke-Elder, 1932) have recently offered evidence that the posterior commissure serves as a pathway for impulses relating to eye-movements, and the close association that exists between the posterior commissure and the medial longitudinal bundle tends to emphasize the importance of the commissure in this respect. On the other hand, this investigation shows that though the mole is blind, it has a very well developed commissure and this fact suggests that the important functions of the posterior commissure may be other than those associated with movements of the eyes.

A comparison between the phylogenetic development of the posterior commissure and that of the cerebellum presents another view regarding the problem of the functions of the commissure. It is recognized that the cerebellum is relatively small in amphibia and reptiles, and this fact has been correlated with the comparatively sluggish habits of these animals. Reference to Table I

shows that in the vertebrates selected for this investigation the development of the posterior commissure as regards size and complexity runs closely parallel with the development of the cerebellum. This parallelism existing between the development of the cerebellum and that of the posterior commissure, and also the fact that the blind mole presents a well-developed commissure, suggests that the more important functions of the commissure may be associated with posture and the integration of body movement rather than with movements of the eyes and visual influences.

SUMMARY

1. The connexions of the posterior commissure have been described in a selected series of vertebrate animals, and in the human foetus and young infant.

2. The dates of myelination of its component fibres in the human have been noted.

3. The degenerative changes resulting from an experimental lesion have been noted and discussed.

4. The bearing of the results of this investigation on the work of other observers has been noted.

5. Deductions that might be drawn from the phylogenetic review have been discussed.

ACKNOWLEDGEMENTS

I would wish to offer my best thanks to Prof. le Gros Clark, whose help with the experimental work has assisted in rounding off what might otherwise have been a very inconclusive investigation.

My colleague Dr E. E. Hewer, who began this investigation with me, was unable owing to illness to pursue it to its conclusion, and I wish to acknowledge her very great help in the arduous work involved in the examination of the serial sections which form the basis of this research.

Finally, grateful acknowledgement is due to the Thomas Smythe Hughes Medical Research Fund and to the Waller Research Fund which have in part paid the expenses incurred in this investigation.

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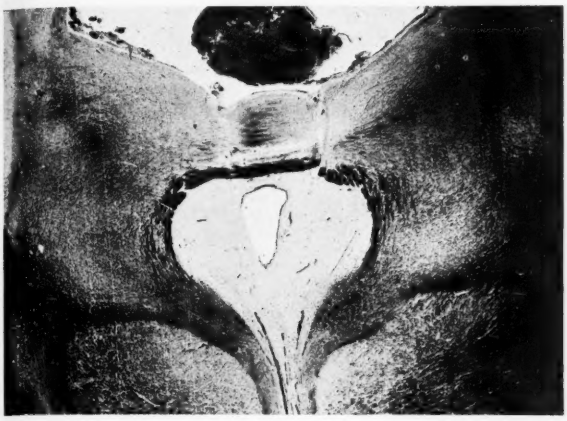

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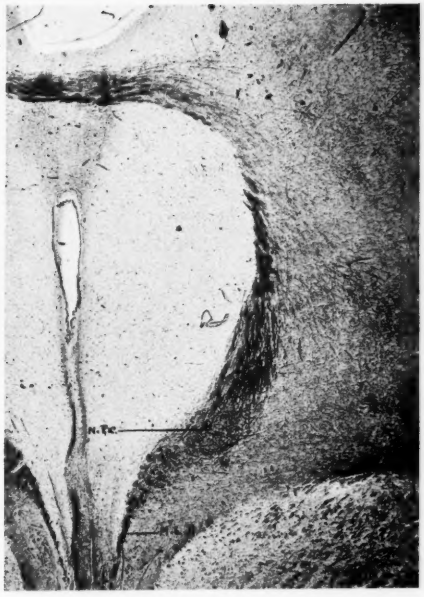

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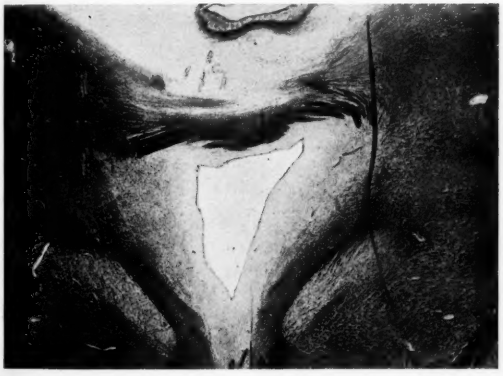

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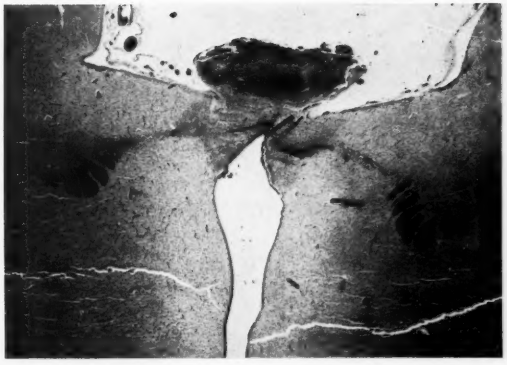

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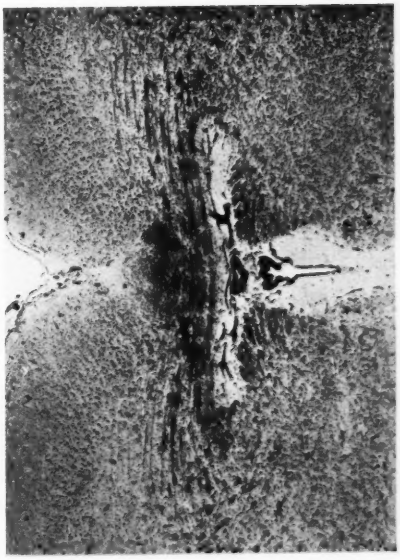

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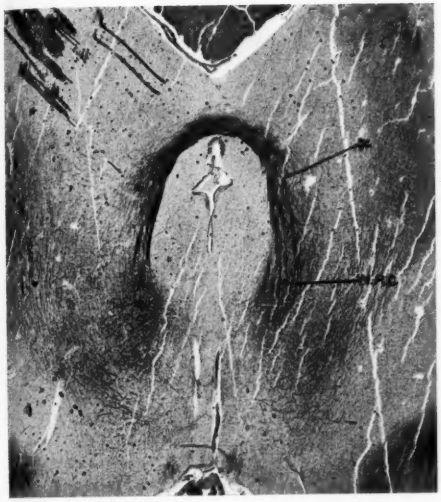

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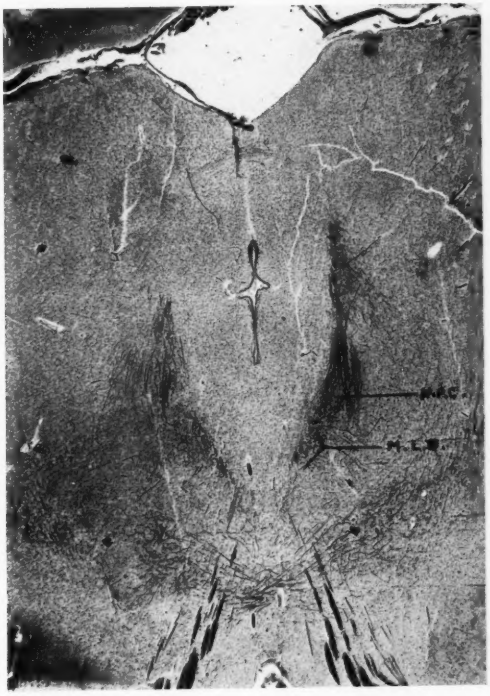

Fig. 2.

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EXPLANATION OF PLATES I–III

PLATE I

Fig. 1. Section through posterior commissure of infant aet. 3 months (2312), showing general arrangement of commissure. ×9·5.

Fig. 2. Section showing coarse commissural fibres arising in nucleus of the posterior commissure (*N.P.C.*) and the close relation with the medial longitudinal bundle (*M.L.B.*). Infant aet. 3 months (2312). ×10.

Fig. 3. Section showing fine fibres in dorsal part of the commissure connecting with the thalamus. Infant aet. 9 months (2296). ×7·5.

Fig. 4. Section showing horizontally directed fibres joining commissure. Infant aet. 8 months (1164). ×7.

Fig. 5. Section through cranial part of the commissure showing connexion with habenular ganglion, and habenulo-peduncular tract. Infant aet. 3 days (2338). ×5. [The commissural fibres are running in a horizontal direction. The three vertical dark streaks are not fibres, two are blood vessels and one is a fold in the section.]

The above figures are photomicrographs of human material prepared by the Weigert-Pal method.

PLATE II

Fig. 1. Section through posterior commissure of petromyzon, showing ipsilateral subcommissural organ connexion (339). ×40.

Fig. 2. Section showing posterior commissure in skate (95). ×6.

Fig. 3. Section showing the posterior commissure in Salamander. *M.R.* = mesocoelic recess. *D.F.* = dorsal fibres. ×25.

Fig. 4. Section (kindly lent by Dr Una Fielding) showing posterior commissure in mole. *M.R.* = mesocoelic recess. ×10.

PLATE III

Fig. 1. Section of brain of 3 weeks old kitten (38); Weigert-Pal preparation, showing myelinated fibres connecting with nucleus of posterior commissure (*N.P.C.*), and also the site of the dorsally placed nucleus (*x*, see text) lying among the commissural fibres. ×8.

Fig. 2. Section of brain of 3 weeks old kitten (38), Weigert-Pal preparation, showing medial longitudinal bundle (*M.L.B.*) arising close to region occupied by cells of the nucleus of the posterior commissure (*N.P.C.*). ×17.

Fig. 3. Section through region of the pons of *Rhesus* monkey (O.M. 145), showing degeneration in fibres of medial longitudinal bundle on same side as the lesion. ×5.

All the figures are photomicrographs of sections made approximately in the coronal plane. The figures in brackets refer to the serial number of each specimen.

OBSERVATIONS ON THE PROBLEM OF THE PROPRIOCEPTIVE INNERVATION OF THE TONGUE

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The problem of the proprioceptive innervation of the tongue still remains unsettled, for the available evidence which bears upon it is conflicting. Langworthy wrote in 1924 that, although hitherto muscle spindles had not been found in the tongue, he was able by Sutton's method to demonstrate their presence in the cat, dog, rat and opossum. Unfortunately, however, he gave no drawings or photographs in support of this finding, and his results still lack confirmation from other sources. It may be noted that Langworthy states in the same paper that muscle spindles are numerous and easily demonstrable in the extra-ocular muscles, whereas it is now generally agreed that, if they exist at all, they are very few and of a primitive type.

In the present study, muscle spindles have been diligently sought in the rabbit's tongue, using pyridine silver and also Bodian's (1936) activitated protargol technique, but with negative results. A search has also been made for them with the use of the pyridine-silver technique in the musculature of the prehensile tongues of *Chamaeleon dilapis* and *Myrmecophaga tridactyla* (where their presence might be reasonably expected), but in these cases, also, none were found. It is perhaps not legitimate to lay much emphasis on these negative findings in view of the relative sparsity of muscle spindles in some types of muscle. It remains possible, also, that proprioceptive impulses from the tongue musculature may be carried by afferent fibres whose nerve endings have no distinctive morphological characters.

If proprioceptive fibres are present in the tongue, there are three possible routes by which they can travel—the lingual, glosso-pharyngeal or hypoglossal nerves. Evidence in favour of the lingual route has been reported by Barron (1936). He cut the lingual, chorda tympani and hypoglossal nerves in cats, rabbits and rats, and recorded action potentials in their peripheral segments by means of an amplifier. No impulses set up by stretching, depressing, touching, burning or chemically stimulating the tongue were found to be transmitted by the hypoglossal nerve. The lingual nerve responded to stretching, touching and burning, and the chorda tympani to chemical stimuli only. Barron concluded that proprioceptive impulses from the tongue are conveyed by the lingual nerve and not by the hypoglossal nerve.

Against this conclusion there is Langworthy's (1924) observation that cutting one or both lingual nerves (or the ninth nerve) produced no apparent ataxia or weakness of the tongue, and it is also well established from clinical observations that no apparent ataxia of the tongue follows extirpation of the Gasserian ganglion or destruction of the sensory root of the trigeminal nerve. It would appear, on these grounds, that the hypoglossal nerve is the only possible route for proprioceptive fibres from the tongue musculature. If this is so, the question arises as to the location of their ganglion cells. There seem to be three possibilities:

(*a*) *The ganglion nodosum of the vagus.* The tenth and twelfth nerves communicate both at their exit from the skull, and through the lingual branch of the vagus to the pharyngeal plexus. (This latter branch is not mentioned in continental text-books.)

(*b*) *The ganglia of the upper four cervical nerves,* since the hypoglossal nerve communicates with the upper loop of the cervical plexus.

(*c*) *Ganglion cells* situated along the course of the hypoglossal nerve.

(1) *The ganglion nodosum.* This source of fibres has been eliminated by Hinsey & Corbin (1934). They cut the hypoglossal in sixteen cats, and, after allowing periods of 10–22 days to elapse, found no degeneration by the Marchi method in the nodose ganglion.

(2) *The root ganglia of the upper four cervical nerves.* This was also eliminated in cats by Hinsey & Corbin in the same group of experiments. But later Corbin *et al.* (1937) in five experiments on *Macaca mulatta* in which the second cervical dorsal root ganglion was removed (a first root ganglion rarely exists in the monkey), found degeneration in the twelfth nerve in all five cases. The degeneration affected only 1–2 % of the fibres. It was, however, traceable distally beyond the branch to the thyrohyoid, thereby proving that the fibres were not derived from the infrahyoid muscles but from the tongue itself. Surprisingly, in two of the five cases, degeneration was also found in the root of the twelfth nerve proximal to its connexion with the second cervical nerve. The passage of a few sensory fibres from the tongue via the descendens hypoglossi to the second cervical ganglion was also found in the hedgehog by Berkelbach van der Sprenkel (1924), who thought they probably came from the hyoglossus and styloglossus muscles. 1–2 % of fibres, however, even if they are all proprioceptive, contrasts markedly with Sherrington's (1898) estimate that one-third to one-half of the myelinated fibres in muscular nerve trunks generally are from cells of the spinal root ganglion.

(3) It therefore appears that, if proprioceptive fibres arise in the tongue in any but the meagre proportion of 1–2 %, they must be served by ganglion cells along the course of the twelfth nerve. Okamura (1936) gave a series of drawings of ganglion cells in the cat's tongue with free terminals which form a network around the adjacent muscle fibres. Tarkhan (1936) cut the twelfth nerve in rabbits, and after allowing time for degeneration, examined the distal end for undegenerated fibres. In one case he found a few scattered fibres

(no percentage given). In another case he found a ganglion near the origin of the descendens hypoglossi, distal to which 50 % of the nerve fibres were undegenerated. He concludes that proprioceptive sensation in the tongue is served either by a definite ganglion or by scattered ganglion cells along the course of the twelfth nerve.

In order to test Tarkhan's assumption, the following experiments were made. In nine rabbits, the hypoglossal was cut a short distance from the base of the skull. When possible the section was made proximal to the origin of the descendens hypoglossi branch. This nerve often does not exist in the rabbit, being then replaced by a fine independent filament from the first cervical nerve. The rabbits were killed at different periods after the operation, viz. 6, 8, 9, 10, 11, 15, 16 and 21 days. Immediately after death the proximal end of the cut nerve was removed, and in two cases also a part of the distal end close to the section. When the portion directly involved by the lesion had been cut away it was not possible to get more than $\frac{1}{2}$–1 cm. length of nerve for examination. The nerves were fixed for 6 hr. in 1 % osmium tetroxide and then washed in water for 3 days. They were dehydrated in graduated ascending concentrations of alcohol, cleaned in xylene, placed in xylene-paraffin, and embedded in paraffin. To avoid extraction of the stain, the time for cleaning was limited to half an hour.

Examination of serial sections of cut nerves. Neither in the short proximal piece of the hypoglossal nerve close to the skull, nor in the peripheral segments removed from midway along its course, were ganglion cells ever found, whether scattered or grouped together. In eight cases no degeneration was found above the section. In one case, in which the nerve had been sectioned 10 days previously, a small bundle of fibres lying beside the main trunk showed complete degeneration. In this instance, however, the presence of all the degenerated fibres together in a separate bundle suggests a source other than the tongue—possibly a loop of connexion with a nerve of cervical origin, but it was not possible to trace their source. Except for this single and doubtful case no support was found for Tarkhan's suggestion that ganglion cells exist along the course of the hypoglossal nerve. In the two cases where the distal end of the cut nerve was examined histologically, degeneration was complete (Figs. 1, 2).

In order further to test the possibility of proprioceptive fibres related to ganglion cells in the course of the hypoglossal nerve, and also to test the suggestion made by some previous observers that proprioceptive fibres accompany the lingual nerve, the following experiment was made. In rabbit No. 6, the lingual nerve was cut on the right side in the submaxillary region, and 10 days later the left hypoglossal nerve was sectioned proximal to the position where ganglion cells on its trunk were described by Tarkhan. The animal was killed 11 days later. Serial sections were made of the right and left sides of the tongue, and stained with pyridine-silver. On the right side numerous motor nerve endings terminating in typical end-plates were found in the muscle fibres. On the other hand, since the lingual nerve had been sectioned,

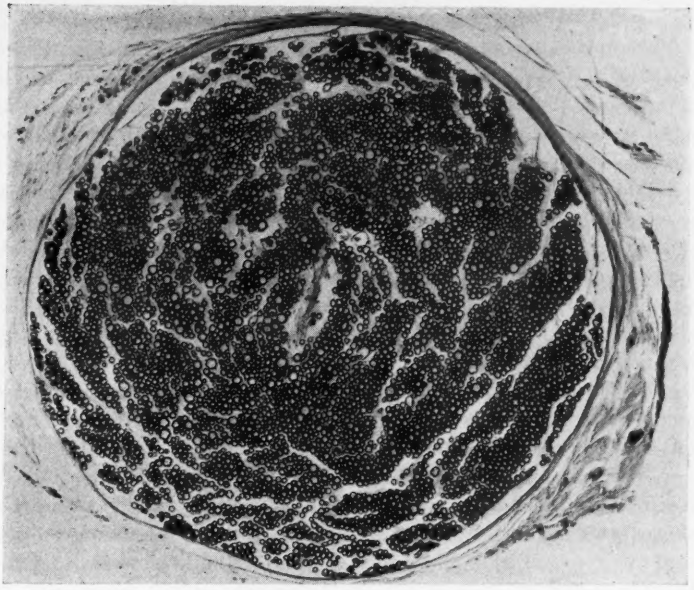

Fig. 1. Section of hypoglossal nerve, proximal to section. (Rabbit 6, killed 11 days after section.) ×155.

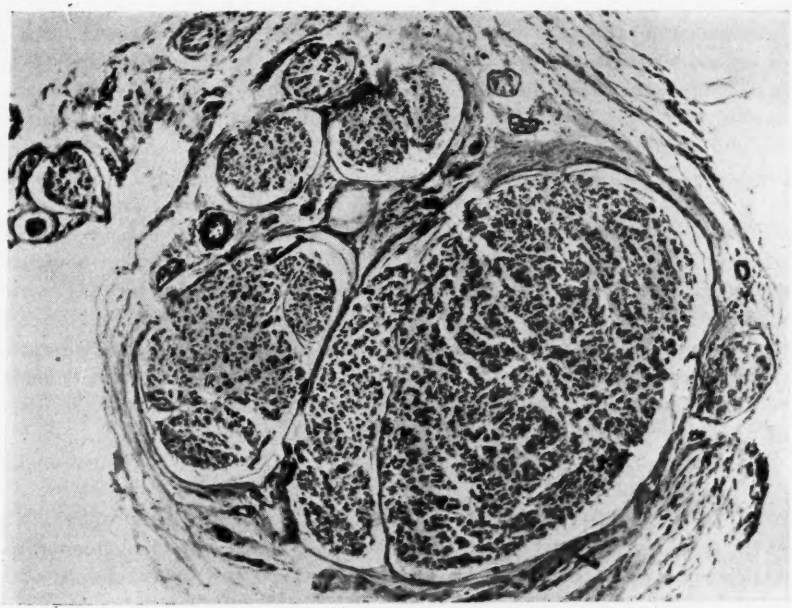

Fig. 2. Section of hypoglossal nerve, distal to section showing complete degeneration. (Rabbit 3, killed 8 days after section.) ×125.

nerve fibres in the mucosa were completely absent. On the left side, the motor terminals of the hypoglossal nerve had undergone total degeneration. No nerve terminals of any kind could be found, even after prolonged study of the serial sections, in relation to the muscle fibres. Fasciculi of lingual nerve fibres were seen in the intermuscular septa of the tongue, and in many cases these could be traced through to the mucous membrane where they terminated in fine endings either immediately deep to the epidermis, or in the deeper layer of the epidermis. Fine nerve fibres were also evident in immediate relation to blood vessels. The fact that on the side of the tongue on which the hypoglossal nerve had been sectioned proximally no nerve terminals at all were found in relation to muscle fibres is strong evidence (1) that no proprioceptive fibres travel in the lingual nerve, and (2) that no proprioceptive fibres have their cells of origin on the trunk of the hypoglossal nerve in its peripheral course in the neck. This is in agreement with the work of Boyd (1937), who made complete serial sections through the heads of full-time rabbit foetuses, and could find no evidence for sensory cells on the course of the hypoglossal as described by Tarkhan, nor any trace of a Froriep's ganglion. Further, no histological evidence was seen of a direct connexion between the intramedullary fibres of the hypoglossal and any cell group other than the nucleus of Stilling.

Another aspect of the question of the proprioceptive innervation of the tongue may be considered. Evidence of the existence of proprioceptive fibres may be provided by the existence of position sense. Langworthy has stated that "human beings are aware of the position of the tongue even when it is held away from the walls of the mouth". This statement was tested in a series of individuals with the assistance of Mr R. G. Macbeth (whose help I wish gratefully to acknowledge). A 5 % freshly made solution of cocaine was applied to the lips, labio-dental groove, floor and roof of the mouth, the tongue and pyriform fossa. This was repeated in 10 min., and if anaesthesia was still light, a 10 % solution was used. With the eyes closed, the tongue was gripped by a forceps and pulled by an observer in various directions. Of eight individuals tested, four were unable to note the position of the tongue or even whether it was moved at all, unless it was pulled to its limit when they were conscious of traction at its base. One individual could interpret upward movement of the tongue but not movements in other directions. Two could interpret the movements correctly in approximately 50 % of trials, and one could interpret correctly every movement. It remains possible that, owing to inadequate cocainization, there was incomplete loss of tactile sensation in those cases in which movements of the tongue could still be recognized.

CONCLUSIONS

The observations recorded above in regard to the proprioceptive innervation of the tongue are negative in their implications. The absence of demonstrable muscle spindles in the tongue musculature so far as this was examined with silver techniques, the failure to identify nerve fibres or nerve cells which might

subserve proprioceptive impulses, and the fact that in a certain proportion of cases all sense of position of the tongue is lost after cocainization of the mucous membrane of the tongue and mouth—all these suggest the possibility that proprioceptive innervation may not exist in the tongue musculature. The complete absence of nerve endings in direct relation to muscle fibres after section of the hypoglossal nerve indicates that, if proprioceptive fibres are indeed present, they must run in the trunk of this nerve. No positive evidence, however, has been found to support Tarkhan's conclusion that such hypothetical proprioceptive fibres have their ganglion cells along the course of the hypoglossal nerve.

SUMMARY

1. The proximal part of the hypoglossal was cut in nine rabbits and time allowed for degeneration, varying from 6 to 21 days. Except for one doubtful instance, no evidence was found to support Tarkhan's suggestion that ganglion cells exist along the course of this nerve.

2. No muscle spindles have been found in the tongue of the rabbit, or in the prehensile tongues of the chamaeleon (*Chamaeleon dilapis*) and the anteater (*Myrmecophaga tridactyla*).

3. The lingual nerve in one rabbit was cut on one side, and the hypoglossal nerve on the other. Nerve terminals in relation to muscle fibres of the tongue were found on the side where the lingual had been cut, but were completely absent on the other side.

4. The mucous membrane of the tongue and mouth was anaesthetized with 5–10 % cocaine in eight individuals. All sense of position of the tongue was lost in four, there was partial loss in three, and no loss in one case.

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THE INNERVATION OF THE OVARY, UTERINE TUBE, TESTIS AND EPIDIDYMIS

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The innervation of the ovary and uterine tube resembles in many respects the nerve supply to the testis and epididymis. The nerves arise from three different sources:

(1) A superior group from the intermesenteric nerves and from the renal plexus.

(2) A middle or intermediate group from the superior hypogastric plexus (pre-sacral nerve) or from the hypogastric nerve.

(3) An inferior group from the inferior hypogastric plexus (pelvic plexus).

(1) *The superior ovarian group.* There are usually two main nerves in the superior ovarian group, an outer and an inner.

The outer arises from the lower part of the renal plexus by two or more rootlets which coalesce to form a single nerve (Fig. 1). This nerve descends along the outer side of the ovarian vessels to the ovary, and may split up into two or three parts which are always connected by delicate branches to the ovarian nerves lying on the inner side of the vessels.

The inner nerve of the superior ovarian group may arise in several ways. It may be attached to the lower end of the intermesenteric nerves and receive a filament from one of the lumbar splanchnic nerves (Fig. 1, left side), or to the upper end of the group of nerves which lies in front of the lower part of the abdominal aorta (abdominal aortic plexus) (Fig. 2). Sometimes it appears to arise from the upper end of the aortic bodies (Fig. 1, right side), which are so closely associated with autonomic nerves in infancy that it is impossible to separate them. In the adult small ganglia may be distinguished amongst the nerves overlying the lower part of the abdominal aorta, and it is probable that in or around the aortic bodies there are small autonomic ganglia which persist after the chromaffin tissue which forms the main mass of the aortic bodies has largely disappeared. Incidentally these bodies do not lie at the level of origin of the inferior mesenteric artery as is usually stated, but are below that level, their lower ends frequently overlying the origins of the common iliac vessels, and their upper ends reaching as high as the origin of the inferior mesenteric artery (Fig. 1).

The inner nerve communicates near its origin with the branches of the renal plexus which arise from the lower ends of the intermesenteric nerves. Its rootlets unite to form a single nerve which converges towards the inner side of the ovarian vessels, and runs downwards with them. If it divides, one

branch may pass to the outer side of the ovarian vessels, or lie between them, where it communicates or unites with the outer nerve (or nerves) of the superior ovarian group.

In a previous article a direct connexion between the testicular nerves and the coeliac or superior mesenteric plexuses was described, and a similar arrangement has been seen in a dissection of the ovarian nerves. The inner of the left superior ovarian nerves arose by two rootlets from the lower ends of the two outermost intermesenteric nerves on the left side, but it had another rootlet which passed upwards and became continuous with the commencement of the superior mesenteric plexus behind the neck of the pancreas (Fig. 1).

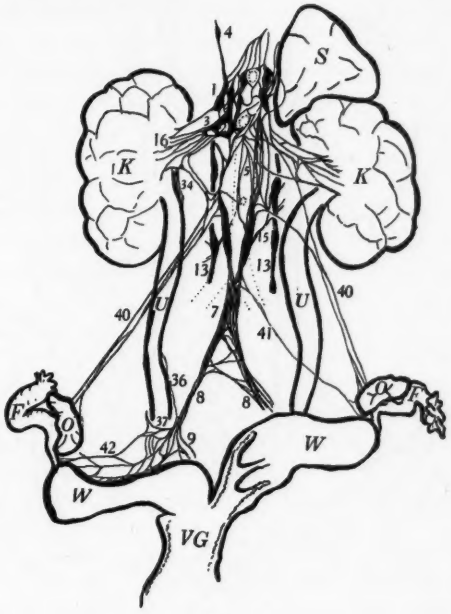

Fig. 1.

Strictly speaking, this branch connecting the coeliac or superior mesenteric plexuses with the ovarian nerves is really one of the intermesenteric nerves, but it merits special attention since it is unusual to be able to distinguish macroscopically such a direct connexion amidst the multiple intercommunications of the autonomic nerves.

The superior ovarian nerves give filaments both to the ovary and to the uterine tube, those to the tube being fine and not numerous.

(2) *The middle or intermediate ovarian nerves* arise from the superior hypogastric plexus or the hypogastric nerve (Figs. 1, 2), being sometimes associated with a twig passing to supply the ureter. Two appears to be the

common number, but in one dissection three nerves were seen, one arising from the superior hypogastric plexus, and two from the hypogastric nerve. The branch from the superior hypogastric plexus may arise directly, running close to the antero-internal aspect of the common and internal iliac vessels, or it may come via a nerve which arises from the superior hypogastric plexus, but lies behind the common and external iliac vessels. This post-arterial nerve, in addition to the ovarian branch, gives one or two twigs to the external iliac artery, and another twig usually enters the Psoas Major, either supplying

Fig. 2.

it or passing through it to unite with one of the branches of the lumbar plexus. Thereafter the nerve splits into several filaments which pass into the thigh alongside the external iliac artery, where their further course has not been investigated[1]. The ovarian nerve itself, whether it comes directly or indirectly (in the way just described) from the superior hypogastric plexus,

[1] Dr J. C. White, of Boston, who recently examined this nerve in three dissections, suggested that it may supply the femoral artery at the point where it gives off its profunda branch. Impulses from this region may play some part in the control of the blood supply to the lower limb. So far this interesting suggestion has not been verified as the limbs had been removed in all the specimens showing the nerve.

passes downwards and outwards, finally breaking up into five or six terminal filaments which supply the ovary and the outer half of the tube. The lower of the middle ovarian nerves arises from the hypogastric nerve, and runs parallel and close to the other nerves described above (Fig. 2). It is usually smaller, and breaks up into filaments which supply the inner half of the tube, and possibly the ovary. In one dissection yet another but smaller nerve came off the hypogastric nerve; it supplied filaments both to the uterus and the inner end of the uterine tube.

All these nerves lie along the postero-lateral wall of the pelvis until they reach the broad ligament. They then turn inwards between the layers of the ligament to reach the ovary, tube, and uterus.

(3) *The inferior ovarian nerves*, three or four in number, arise directly from the hypogastric plexus or lower end of the hypogastric nerve (Fig. 1). They run upward between the layers of the broad ligament, one lying close to the uterine margin and to the anastomosis between the uterine and ovarian arteries, but the others lie at a distance from these vessels, nearer the side wall of the pelvis. They communicate by cross-branches, and are associated nearer their origin with the lowest ureteric nerves, while the innermost nerve of the group gives off tiny branches to the uterus. These nerves innervate the uterine tube, and are attached to its inner half, but delicate filaments can be traced outwards across the ampulla. None was detected entering the ovary.

It is interesting to speculate as to whether the ovary and uterine tube receive a nerve supply from both parts of the autonomic nervous system, and if they do, whether the supplies are mixed up in the various nerves or are confined to separate pathways. By analogy with the hollow viscera it is almost certain that the uterine tube receives a supply from both sympathetic and parasympathetic, but a double innervation cannot be postulated with the same degree of certainty for the ovary.

If the ovary does receive a nerve supply from both sympathetic and parasympathetic, it is conceivable that both might come from above through the superior ovarian nerves, because the developing ovary draws down its nerve supply with it when it descends from the renal region to the pelvis. There is nothing to prevent its receiving a secondary nerve supply, which might contain both sympathetic and parasympathetic elements, from the pelvic plexus, yet no nerve filaments from this source could be detected entering the organ. Thus it is possible that, as in the case of the testis and epididymis, the ovary and oviduct may receive separate nerve supplies. But as the epididymis and uterine tube are not homologous structures any resemblance in the matter of nerve supplies, though interesting, is coincidental.

If the above supposition is correct, then the entire ovarian nerve supply may be contained in the superior and middle ovarian nerves, and they would be more correctly termed superior and inferior ovarian nerves; those described as the inferior ovarian nerves would then be designated as tubal, or tubo-uterine, and not ovarian. If this possibility is accepted, the next problem

that arises is the actual nature of the nerve-supply to the ovary, and by simple reasoning it can be deduced that the ovarian nerves must be mainly or even wholly sympathetic in nature, since sympathetic elements preponderate greatly in the upper abdominal autonomic plexuses—unless the organ receives an undue proportion of the available parasympathetic vagal fibres, compared with the other viscera supplied, which is unlikely. In making this statement it is assumed that the presence of parasympathetic fibres in the posterior nerve roots of the thoraco-lumbar spinal nerves has not been proved, and that the vagus carries the parasympathetic supply for most of the abdominal viscera.

The uterine tube certainly receives a nerve supply from the hypogastric nerve and pelvic plexus, and it may receive delicate twigs from the superior ovarian nerves. The former may be mainly parasympathetic and the latter sympathetic in nature. This arrangement is suggested because it is more reasonable to suppose that the parasympathetic nerve supply to organs such as the uterus and tube, developed from the caudal ends of the Müllerian ducts, should emerge in the sacral rather than in the cranial outflow. It has already been shown (Mitchell, 1935) in the case of the distal colon that a like arrangement probably exists—namely, that the parasympathetic nerves supplying this part of the bowel arise directly from the hypogastric plexuses and nerves and pursue an independent course, streaming upwards across the line of the branches descending from the inferior mesenteric plexus. But in addition certain indirect evidence may be adduced in favour of the suggestion that the sympathetic and parasympathetic supplies are separate. Cotte, Learmonth, Fontaine and Herrmann, Reeb, and others have found that resection of the superior hypogastric plexus (presacral neurectomy) in the female does not produce sterility, and that a normal uterine pregnancy and labour may result. Fertilization and the early stages of development normally occur within the tube, and the zygote ultimately reaches the uterine cavity as a result of muscular and ciliary action. It is conceivable that an ovum could be wafted into the uterine cavity by the agency of the ciliary current alone, even though the uterine tube was completely paralysed, but it is rational to suppose that it will be more certain to reach the uterus if the tubal musculature retains its power of regulated contractility. If the parasympathetic supply to the tube is destroyed it may dilate owing to the unbalanced sympathetic effect, and though some inherent power of contractility may remain, as in other unstriped muscular structures after destruction of their parasympathetic supply, it is probable that an ovum, and particularly a larger fertilized ovum in the early stages of development, would be less likely to reach the uterine cavity. Under these circumstances the risks of ectopic gestation would be increased, but so far this complication has not been recorded following resection of the superior hypogastric plexus (Reeb, 1937), and so it is likely that the parasympathetic fibres for the tubes reach the pelvic plexuses by some other route, the pelvic splanchnics in that case being the obvious pathway: of course they might lie in the superior ovarian nerves, but, for reasons already mentioned, it is unlikely

(*a*) that these nerves convey many (if any) parasympathetic fibres, and (*b*) that the parasympathetic supply of organs developing from the caudal ends of the Müllerian ducts would emerge in the cranial outflow when the sacral outflow is so much more convenient. There is thus a certain amount of evidence, both direct and indirect, that the parasympathetic supply for the uterine tubes emerges in the pelvic splanchnic nerves.

Investigations into the innervation of the testis and epididymis have already been published by me in this *Journal*, and I do not intend to repeat the observations therein recorded. But since then several additional facts have come to light.

In the previous article several variations in the mode of origin of the middle testicular nerves were recorded, and in two cases another arrangement was suspected, though a successful dissection of the pathway, without breakage of the delicate nerves, was not accomplished until recently. It has now been traced on the left side of one specimen, and it is rather unusual (Fig. 3).

The nerve had two heads of origin: (1) a single rootlet from the lower part of the left renal plexus, and (2) two delicate filaments from the middle lumbar splanchnic nerves; in this case four lumbar splanchnic nerves were present arising from the upper half of the lumbar part of the left sympathetic trunk (Fig. 4). The nerve so formed descended almost vertically as an isolated strand, lying in front of the Psoas Major and lateral to the abdominal aorta. At the level of the bifurcation of the aorta it communicated by delicate filaments with the superior hypogastric and inferior mesenteric plexuses (Fig. 3). Having crossed the left common iliac artery it ran along the inner margin of the obliterated hypogastric artery until it came into contact with the vas deferens, which it accompanied thereafter as far as the testicle. In the pelvic part of its course it had several important connexions: (1) At the level of the pelvic brim it gave off a filament which joined the upper end of the sacral part of the left sympathetic trunk (Fig. 4). (2) Near the internal inguinal ring two very fine filaments united it to the pelvic plexus (Figs. 3, 4). (3) It communicated with the middle and inferior ureteric nerves (Fig. 3). (4) Near the internal inguinal ring it received a small branch formed by the coalescence of three filaments from the left genito-femoral nerve (Fig. 4). (5) It has been found several times that a leash of autonomic nerve fibres is located behind the common and external iliac arteries (Fig. 4). This bundle of nerves arises from the superior hypogastric plexus, usually as a single strand, which soon breaks up into three or four filaments. In this dissection one of these filaments became directly continuous with the middle testicular nerve. The others passed alongside the artery into the thigh where their subsequent course and distribution has not been studied. As can be seen from the figure (Fig. 4), the nerve also communicated with the left hypogastric nerve and with the left lateral sympathetic trunk about the level of the lumbosacral junction.

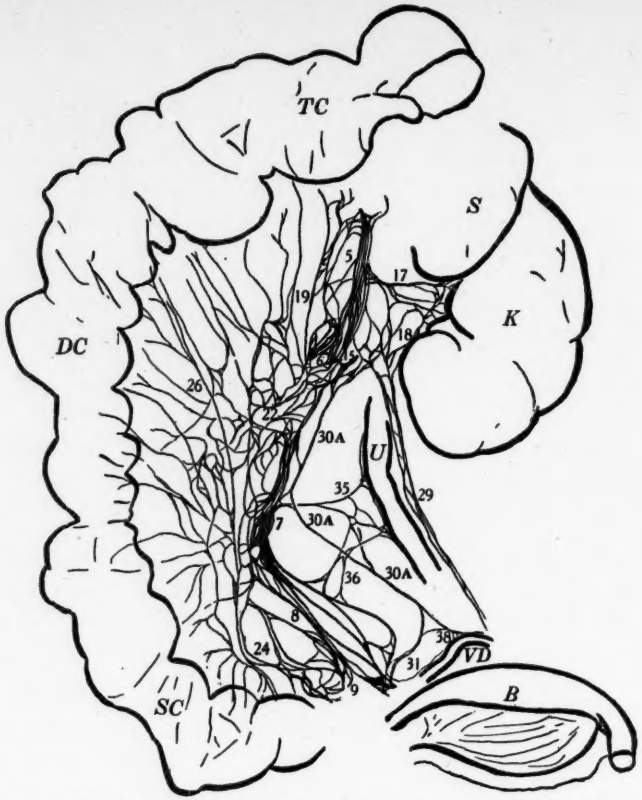

Fig. 3. The descending colon has been drawn over towards the right side.

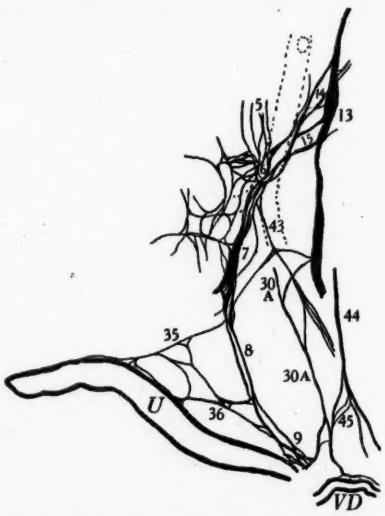

Fig. 4. The left kidney has been removed and the ureter drawn over to the right side in order to expose the underlying nerves.

Having come into contact with the vas deferens the middle testicular nerve thereafter descended alongside that structure to the testis and epididymis. It was not discovered whether it supplied the testis or epididymis alone, or both, but it certainly supplied filaments to the vas deferens.

It is probable that this interesting but complicated pathway is not uncommon, as I believe that it has been present in three out of fifteen male dissections, though it has only been traced completely without breakages in one specimen. And it is necessary to emphasize that, owing to the delicacy of the fibres and the difficulties of dissection, any figure tends to underestimate rather than overestimate the frequency of the arrangement.

Another observation, this time a clinical one, is worthy of record. Learmonth once observed that a patient, anaesthetic from the ninth thoracic segment downwards as a result of a spinal anaesthetic, retained normal testicular sensibility. Two years ago, when performing an orchidectomy for malignant disease under a spinal anaesthetic, one repeated Learmonth's observation, with almost identical results. The patient, an intelligent man aged 36, still retained testicular sensation when the trunk was anaesthetic as high as the tenth thoracic segment. When the anaesthesia had spread two segments higher testicular sensation was dulled, though not abolished, but when it had reached its maximum about the level of the fifth thoracic segment no sensation remained, and even the latter stages of the operation, involving traction on the cord and testicular vessels gave rise to no pain. It would therefore appear that some at least of the testicular afferents enter the cord at a higher level than the ninth or tenth thoracic segments.

SUMMARY

1. The nerves to the ovary and uterine tube arise from three different sources:

(*a*) A superior group from the intermesenteric nerves and from the renal plexus.

(*b*) A middle or intermediate group from the superior hypogastric plexus or from the hypogastric nerve.

(*c*) An inferior group from the inferior hypogastric plexus.

2. The exact position of the aortic bodies is defined.

3. A direct connexion between the superior ovarian nerves and the coeliac or superior mesenteric plexuses is sometimes demonstrable.

4. It is possible that the nerve supply to the ovary may be mainly sympathetic in nature, and confined to those nerves described above as the superior and middle ovarian nerves. The inferior ovarian nerves supply filaments both to the uterus and tubes, but few (if any) to the ovaries; it is therefore suggested that they should be designated as tubal or tubo-uterine, and not ovarian.

5. Evidence, both direct and indirect, is adduced in support of the view that the parasympathetic supply for the uterine tubes emerges in the pelvic splanchnic nerves.

6. An interesting testicular nerve is described and its connexions illustrated.

7. Attention is drawn to a bundle of autonomic nerves which is occasionally found behind the common and external iliac vessels.

8. Testicular afferents apparently enter the cord at a higher level than is generally stated.

I am deeply indebted to Prof. A. Low who has confirmed all anatomical findings by examination of the actual dissections at various stages; and I wish to record my thanks both to him and to Prof. J. R. Learmonth for much valued criticism and advice. The expenses of this investigation were defrayed with the aid of a grant from the Medical Research Council.

EXPLANATION OF FIGURES

The numbers have been selected to conform with those used in plates and text-figures illustrating previous articles. The absence of certain numbers indicates that the corresponding nerves were not visible in the photographs from which the drawings for this article were made.

(1) Semilunar ganglion.
(2) Aortico-renal ganglion.
(3) Renal ganglion.
(4) Phrenic ganglion.
(5) Intermesenteric nerves.
(6) Inferior mesenteric plexus.
(7) Superior hypogastric plexus (pre-sacral nerve).
(8) Hypogastric nerves.
(9) Inferior hypogastric (pelvic) plexus.
(13) Lumbar sympathetic ganglionated trunk.
(14) Rami passing to intermesenteric nerves (upper group of lumbar splanchnic nerves).
(15) Rami passing to abdominal aortic or superior hypogastric plexus (lower group of lumbar splanchnic nerves).
(16) Nerves from aortico-renal ganglion to renal plexus.
(17) Branches from intermesenteric nerves to renal plexus.
(18) Nerves connecting renal plexus with intermesenteric nerves and inferior mesenteric plexus.
(19) Nerve loop connecting coeliac and superior mesenteric plexuses to inferior mesenteric plexus.
(22) Colonic nerves accompanying inferior mesenteric artery and its branches.
(24) Short colonic branches from hypogastric nerve and inferior hypogastric plexus.
(26) Long colonic branch from inferior hypogastric plexus.
(29) Superior spermatic nerves.
(30) Middle spermatic nerve(s).
(30A) Spermatic nerve described on p. 513 of text.
(31) Inferior spermatic nerves.
(34) Superior ureteral nerve(s).
(35) Middle ureteral nerve(s).
(36) Inferior ureteral nerves.
(37) Nerve loop in front of lower end of ureter.
(38) Nerves to vas deferens.
(40) Superior ovarian nerves.
(41) Middle ovarian nerve(s).

(42) Inferior ovarian nerves.
(43) Nerve(s) lying behind common and external iliac vessels, described on p. 510 of text.
(44) Genito-femoral nerve.
(45) Communications between genito-femoral nerve and nerves to testis and vas deferens.

B Bladder (split in median sagittal plane).
F Uterine tube.
K Kidney.
O Ovary.
S Suprarenal.
U Ureter.
VD Vas deferens.
VG Vagina (cut in median sagittal plane).
W Uterus (cut in median sagittal plane).
TC Transverse colon.
DC Descending colon.
SC Sigmoid colon.
IM Inferior mesenteric artery.

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ON THE LOCALIZATION OF NERVE CENTRES OF THE EXTRINSIC OCULAR MUSCLES IN THE OCULOMOTOR NUCLEUS

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INTRODUCTION AND LITERATURE

The individual nerve centres of the extrinsic ocular muscles in the oculomotor nucleus in mammals have been a subject of an extensive and elaborate study by various investigators whose results are contradictory.

Le Gros Clark (1926) states that "the literature dealing with the oculomotor nucleus of mammals has accumulated to voluminous proportions and there still remains considerable doubt regarding the localization of function among the constituent cells of the group, and even regarding the actual constitution of the nucleus itself. He also adds that "of the later works dealing with these subjects, those of Brouwer and Latumeten gave an extensive summary of the investigations of previous authors and their own conclusions remain contradictory on important questions".

Among those who contributed to our knowledge about the different descriptions, and the detailed comparative anatomy, as well as the question of localization of the centres of the oculomotor nucleus of different mammals, are: Perlia, 1889; Bach, 1899; Edinger, 1904; Tsuchida, 1906; Brouwer, 1918; Frank, 1921; Hunter, 1923; Le Gros Clark, 1924, 1926; Latumeten, 1924; and Woollard, 1925.

Le Gros Clark's excellent paper on the oculomotor nucleus of mammals comprises a full and satisfactory account of all the previous work done on the subject. It is all that is necessary for the present communication.

METHODS AND RESULTS

In the present communication it is intended first to give a description of the oculomotor nucleus in the cat, and secondly, to report the degeneration results following either enucleation of the eyeball as a whole, or the avulsion of individual muscles.

The nucleus, as has been described in various mammals by many authors (Le Gros Clark and others), lies ventral to the central grey matter in the floor of the aqueduct of Sylvius. In a horizontal serial section it is made up of two columns of cells, one on either side of the median raphe. Each column, usually called the lateral nucleus, extends from the distal end of the third ventricle to about the level of the caudal margin of the superior colliculus (see Figs. 1–3).

About the middle third of the nucleus—in horizontal serial sections—the maximum length of the lateral nucleus in a dorso-ventral direction in an adult cat of about 2 kg. body weight, amounts to 2–2·40 mm. Its widest side to side diameter varies from 0·9 to 1 mm.

The two lateral nuclei are widely separated from each other, cephalad as well as ventrally. Their distal halves, however, come closer together towards the middle line, and in the dorsal part the cells of one nucleus come into contact with those of the other nucleus.

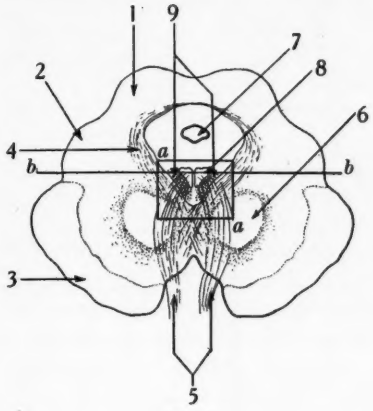

Fig. 1.

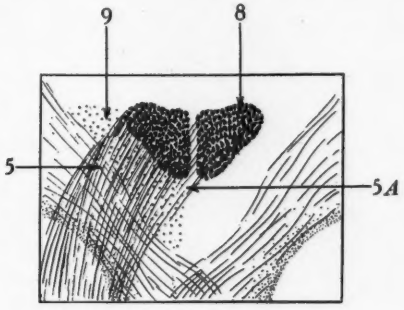

Fig. 2.

Fig. 1. A diagram of a transverse section through the midbrain of a cat at the level of the superior corpora quadrigemina, showing the oculomotor nucleus and its surrounding structures. 1, superior corpora quadrigemina; 2, medial geniculate body; 3, cerebral bundle; 4, tecto-spinal tract; 5, the two oculomotor nerves; 6, red nucleus; 7, aqueduct cerebri; 8, oculo-motor nucleus; 9, medial longitudinal bundle; *a–a*, the square enlarged in Fig. 2; *b–b*, the site of Figs. 3 and 4.

Fig. 2. A diagrammatic enlargement of the square *a–a* in Fig. 1, to show the oculomotor nerve of the right side arising from both halves of the nucleus. The medial fibres of the right oculomotor nerve arise from the medial part of the opposite or left half of the nucleus, and its lateral ones spring from the lateral portion of the same or right half of the nucleus.. 5, right oculomotor nerve (lateral part); 5 *A*, right oculomotor nerve (medial part); 8, left half of the oculo-motor nucleus; 9, medial longitudinal bundle.

Each lateral column consists of a dorsal and a ventral nucleus. The dorsal nucleus which is pyriform in shape has its broader part towards the trochlear nucleus. The ventral nucleus extends more caudally than the dorsal nucleus, and so only in its anterior portion is it covered by the dorsal nucleus. In contradistinction to the dorsal nucleus which appears semioval in transverse section, the ventral nucleus has a triangular shape.

There is a central caudal nucleus (Tsuchida) lying in the median plane between the distal ends of the dorsal nucleus of both sides (see Fig. 3).

A Perlia median nucleus was not observed, while, on the other hand, a well-developed Edinger-Westphal nucleus is always seen medial in its caudal part,

and ventral in its rostral part to the anterior extremity of the ventral nucleus. In its distal part the Edinger-Westphal nucleus partially blends in the median plane with that of the opposite side.

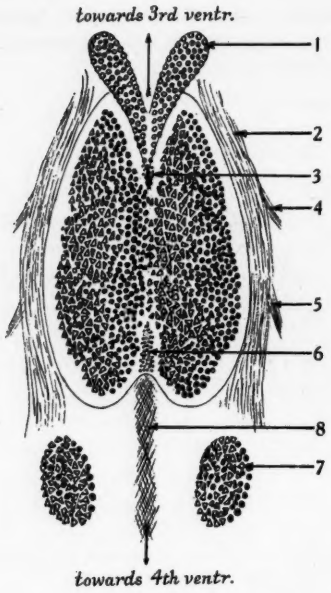

Fig. 3.

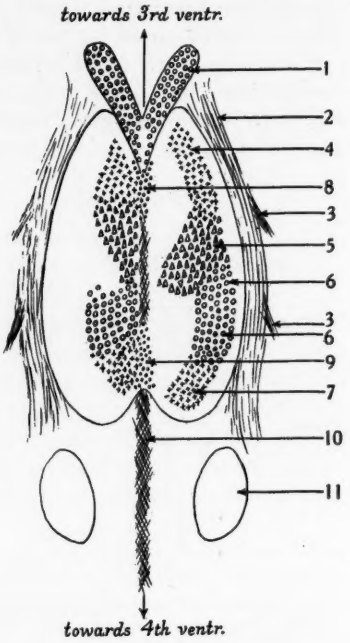

Fig. 4.

Fig. 3. A horizontal section through the oculomotor nucleus—at *b–b* as seen in Fig. 1—to show the result of right enucleation. Healthy cells appear triangular, while the cells with chromatolysis are represented by circles. There is chromatolysis in both sides of the nucleus, i.e. in both lateral part of the same or right half, and medial portion of the opposite or left half of the nucleus. 1, Edinger-Westphal nucleus; 2, medial longitudinal bundle; 3, median raphe; 4, 5, tecto-spinal tract; 6, Tsuchida nucleus; 7, trochlear nucleus; 8, median raphe.

Fig. 4. A composite drawing from the serial sections of avulsion of individual muscles of the left eye to show the areas of chromatolysis corresponding to the nerve centres of the individual extrinsic ocular muscles in the oculomotor nucleus in a horizontal section through its middle (see Fig. 1, *b–b*). These areas are indistinctly localized from one another in the nucleus; and each muscle is bilaterally represented in the two halves of the nucleus and indicated by different marks. 1, Edinger-Westphal nucleus; 2, medial longitudinal bundle; 3, tecto-spinal tract; 4, centre for superior levator palpabrae and superior rectus muscles; 5, centre for medial rectus muscle; 6, centre for inferior oblique muscle; 7, centre for inferior rectus muscle; 8, median raphe; 9, Tsuchida nucleus; 10, median raphe; 11, trochlear nucleus.

The lateral column of each oculomotor nucleus seems to be connected with a bridge of grey matter with the trochlear nucleus. This makes it difficult to recognize the boundary between the two nuclei in transverse sections. The trochlear nucleus, however, is recognized by being laterally embedded in a

concavity in the posterior longitudinal bundle. This can be clearly demonstrated in horizontal sections where the limbs of both nuclei can be distinctly seen from each other (see Figs. 3, 4).

EXPERIMENTAL OBSERVATIONS

Cats were anaesthetized with intraperitoneal injections of dial (0·45–0·50 c.c. per kg. body weight).

The left eye was enucleated in two cats; in another pair of animals the right eye was enucleated. Avulsion of individual ocular muscles was performed in ten cats. The animals were generally killed after a period of about 3 weeks.

The midbrain was, in all cases, fixed in absolute alcohol and stained with either toluidine blue or thionine.

Results

Examination of midbrain of cats whose eyes were enucleated showed degenerative changes in the way of chromatolysis of Nissl's granules in about two-thirds of the corresponding oculomotor nucleus. The rest of the cells (viz. about one-third of the nucleus) appeared quite healthy and were more or less uniformly distributed throughout the nucleus (see Fig. 3).

In the oculomotor nucleus of the opposite side about one-third of the cells exhibited chromatolytic changes.

From this one is justified in concluding that the fibres of the third nerve arise from the oculomotor nucleus of both sides.

Examination of the trochlear nuclei showed chromatolysis of most of the cells of the nucleus of the opposite side, and still more of some of the cells of that of the corresponding side.

A midbrain of a cat which was cut serially and horizontally and stained with silver shows decussation of the medial fibres of the oculomotor nerve—which are about one-third of its fibres—in the region of the nuclei as well as ventral to them, a finding which coincides with the results of degeneration in the region of this nucleus (see Fig. 2). Such a decussation does not exist between the two trochlear nuclei. The degenerative changes in the fourth nerve nuclei may be thus explained: it may be that a few of the fibres of the fourth nerve do not enter into decussation in the anterior medullary velum or that each trochlear nucleus contributes fibres to the oculomotor nerve of the opposite side.

Midbrains of cats in which avulsion of individual muscles was performed showed that most of the extrinsic ocular muscles are represented on both sides of the nucleus. The most medial cells are those whose fibres usually decussate. Each muscle seems, therefore, to receive a nerve supply from a laterally situated group of cells on its own side and as well from a contralateral group placed nearer to the median plane and level with or sometimes more rostral than the first group (see Fig. 3).

Rostro-caudally the muscles are represented in the oculomotor nucleus in the following order: superior levator palpabrae and superior rectus, inferior oblique, medial rectus, and inferior rectus. The inferior oblique lies lateral more than rostral (see Fig. 4).

DISCUSSION

The oculomotor nucleus, in the cat, is a well-developed, and much elaborated nucleus. The fundamental clear division into dorsal and ventral nuclei found in simply constructed oculomotor nuclei of lower mammals is not distinctly seen in all the serial horizontal sections in the cat. The paramedian group which is strikingly evident in *Tupaia*, for example, cannot be made out in any of our serial sections. The median raphe which separates the two lateral nuclei is a narrow space encroached upon by several cells.

In support of this Le Gros Clark writes: "With the progressive elaboration and increasing complexity of the oculomotor nucleus, associated possibly with such factors as the crowding together of the cells by surrounding structures (e.g. the posterior longitudinal bundle), these constituent parts become more and more difficult of recognition as anatomical subdivisions capable of ready identification."

It is natural, therefore, in the present investigation to find that the areas of chromatolysis in the oculomotor nucleus corresponding to removed extrinsic ocular muscles are indistinctly localized from the rest of the cells of the nucleus. This indistinct localization becomes more apparent in the centres of muscles which move the eyeball in more than one direction, e.g. the superior rectus which moves the eye upwards and medially has a less localized centre than that of the levator palpabrae which moves the eye upwards only.

In the morphology, there are no definite statements of any help in connexion with the question of functional localization in the oculomotor nucleus.

Some authors maintain that the localization of individual extrinsic ocular muscles is fairly distinct in the nucleus, while others (e.g. Clark) believe that each muscle receives nerve fibres from the cells distributed all over the nucleus. A few of those who are in favour of the presence of localization differ greatly in regard to the position assigned for the different muscles, as well to the degree of separate localization. Generally most investigators believe that the balance of evidence seems to be in favour of a certain degree of localization.

On the other hand, there are those who believe in group localization of the muscles rather than in their individual representation. They assume that there is a dorsal group for upward movement, and a ventral one for downward movement.

The findings in the present communication, though, have shown a certain degree of individual localization, yet this disagrees in no way with the idea of group localization, which is nothing more than a generalized collective form of individual localization. This latter is simply a further stage of the former, i.e. group localization.

As seen in the diagrams, the levator palpabrae superioris, superior rectus, and inferior oblique muscles which all have in common the power of upward movements of the eye, lie in successive continuity in the dorsal nucleus. The centre for the inferior rectus muscle extends in the ventral nucleus both medially to encroach on the centre of the medial rectus muscle, and latero-caudally to such an extent that in part it approaches the trochlear nucleus of the corresponding side. This is probably because this muscle can move the eyeball medially and downwards.

The clinical and pathological observations are in favour of individual localization. In cases of meningitis, tumours, or other pathological conditions, paralysis may either affect one muscle, or, as in cases of progressive lesions, it extends in a successive order to the muscles (Ingvar). If there is no individual localization, parts of the muscles concerned will be affected by the lesion to about the same degree and not individual muscles in successive order as actually happens.

CONCLUSIONS

1. The oculomotor nucleus in the cat is a well-developed nucleus whose subdivisions are indistinctly demonstrable. A paramedian nucleus is missing.

2. The Edinger-Westphal nucleus is clearly seen, one on each side. The central nucleus of Perlia in the cat is concerned with the nerve supply to the medial rectus muscle. The cells of the Tsuchida nucleus resemble those of the Edinger-Westphal cells in size and shape.

3. Enucleation experiments resulted in chromatolysis mainly in the cells of the nucleus of the same side and to a minor degree in those of the opposite side. Decussation of the fibres of the oculomotor nerve is therefore confirmed.

4. Avulsion of individual muscles resulted in chromatolysis in certain areas indistinctly localized from the rest of the cells of the nucleus. The chromatolysis is often seen on both sides.

5. After enucleation experiments, chromatolysis has been observed in both trochlear nuclei, but more pronounced on the opposite side of the operation.

I wish to express my best thanks to my Professor, Dr D. E. Derry, for his kind supervision, as well as his invaluable guidance and criticism, Dr A. Girgis for his criticism and help, and Dr B. Boulgakow for all the help and facilities he offered me.

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ON THE PRESENCE OF SENSORY FIBRES IN THE OCULAR NERVES

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INTRODUCTION AND LITERATURE

It was formerly believed that the third, fourth, and sixth cranial nerves contain only motor fibres. The extrinsic ocular muscles, like all other forms of muscle, possess a sensory nerve supply, and sensory endings have been described in them by several authors (Sherrington and others). Whether the sensory fibres to these muscles come out from the brain incorporated in the ocular nerves, whether they join them peripherally, or whether they enter the muscles separately, has been considered by various investigators.

Sherrington (1897 and 1898) was the first to record that the afferents from the ocular muscles are contained within the third, fourth, and sixth nerves. He found that section of these nerves results in degeneration of all the myelinated fibres in the ocular muscles. He also found that section of both trigeminal and optic nerves did not considerably depress the tonus of the extrinsic muscles of the eye.

In 1910 Tozer & Sherrington found that in the cat, rabbit and monkey, division of either the third, fourth, or sixth nerves causes degeneration of all the motor and sensory endings in the muscles supplied by the severed nerve. After section of the ophthalmic division of the fifth only, all endings in the ocular muscles exhibited a normal appearance. The authors, therefore, concluded that the third, fourth, and sixth nerves as they leave the brain are afferent-efferent.

Freeman (1925, 1927), after removal of the whole orbital contents in four cats, found that the mesencephalic root on the operated side and at the level of the oculomotor nucleus was slightly degenerated. On the opposite side, degeneration of the same root was found to be at the level of the nucleus of the fourth. In another cat, which he used as control, he merely enucleated the eyeball. He found no difference on either side, either between the cells of the mesencephalic roots or those of the motor nuclei. He finally assumed that the mesencephalic root supplies the proprioceptive fibres not only to the muscles of mastication, but also to the extra-ocular muscles.

Woollard (1931) in a study on the nerve fibres and endings in the ocular muscles confirms the presence in these muscles of two kinds of fibres, thick medullated, thin medullated and non-medullated.

After section of the oculomotor nerve in a rabbit, he found chromatolysis of the mesencephalic cells on the side of the operation, but the mesencephalic

root on the opposite side was quite normal. He concluded that the finer nerve fibres seen in the ocular muscles, and regarded by him as sensory, have their origin in the mesencephalic root of the fifth.

Freeman & Woollard, however, declined to make any suggestion about the course of these fibres towards their destination.

Tarkhan (1934) states that the sensory fibres of the third nerve arise from the cells of the mesencephalic nucleus of the fifth in the region of the superior colliculus, and run ventrally with the tecto-spinal tract to join the motor fibres of the third nerve ventral to their origin from the motor nucleus. The sensory fibres of the fourth nerve arise from the cells of the mesencephalic nucleus implanted on the course and entrance of the fourth nerve into the anterior medullary velum. The author suggests the possibility that the afferent fibres of the external rectus muscle may arise as well from cells of the mesencephalic nucleus and accompany the tecto-spinal tract as far as the level of the abducent nucleus, where they then may join the rootlets of the abducent nerve.

The evidences brought forward in this investigation speak most for a sensori-motor nature of the ocular nerves.

It is generally admitted that central stimulation of afferent fibres evokes various generalized reflex reactions. Assuming that the ocular nerves are sensori-motor, one is justified in expecting that the central stimulation of these nerves would result in some apparent form of reflex. The question, therefore, arose whether such a rise in blood pressure can be obtained on central stimulation of the ocular nerves which have long been regarded by anatomists as purely motor.

In the present investigation we made use of these reflexes with the purpose of adding further evidence on the presence of sensory fibres in the ocular nerves. If it is true that the ocular nerves are sensori-motor we should be able to obtain reflex reactions on central stimulation of these nerves.

METHODS AND RESULTS

Our aim in the following experiments was to stimulate the ocular nerves intradurally before they receive any connexion from the Gasserian ganglion. Cats were first tried. It was, however, found extremely difficult to obtain reliable results on these animals. The length of the nerve between the oculomotor sulcus, and the cavernous sinus is not sufficient for electrical stimulation of the nerve without being assured that no spread of current has taken place. Therefore, dogs were chosen in preference to cats. The animal was anaesthetized with a dose of chloralose, 0·08 g. per kg. body weight given intravenously.

The temporal fossa was exposed and a trephine was made on the left side of the skull. The corresponding cerebral hemisphere was completely exposed, and this exposure extended forward to the orbital cavity. In this way a good view of the third and fourth nerves is always obtainable on lifting the cerebral hemisphere. A faradic current was used for stimulation, followed later by a mechanical stimulation of the same nerve. The blood pressure in the carotid

artery was recorded on a kymograph. One is bound to meet plenty of difficulties during such an experiment. Haemorrhage from the diploe of bone has been a great handicap in some of the experiments. It was controlled by bone wax. Oozing of blood and tissue fluids in the region of the interpeduncular fossa has to be continuously dried with cotton swabs in most experiments. The mere holding of the dura mater with a pair of forceps, as well as the uplifting of the cerebral cortex with a spatula, was quite often immediately followed by a rise of blood pressure. When possible we have avoided holding the cut dura mater, and sometimes we have anaesthetized it by painting it locally with a

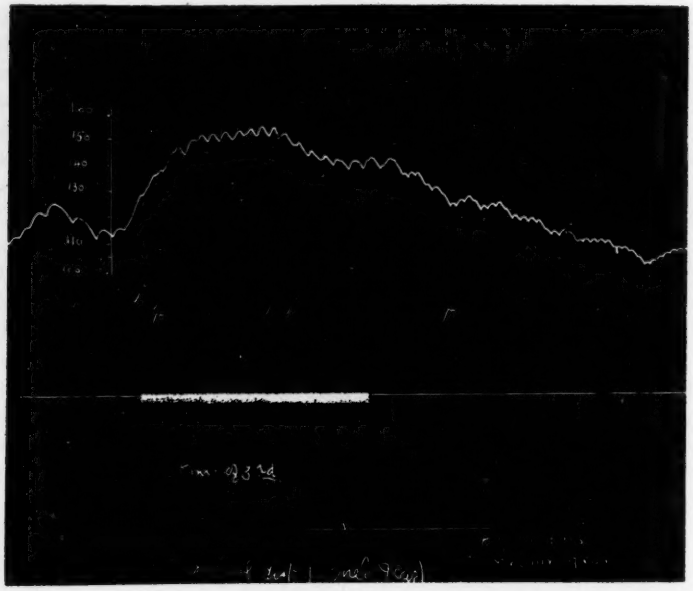

Fig. 1. A graphic record which shows a rise in the blood pressure of a dog of about 50 mm. of Hg on electrical stimulation of the oculomotor nerve intradurally.

solution of 1 % syncaine. Whenever a rise of blood pressure occurred on lifting the cerebral cortex or hemisphere we waited, with the cerebrum-lifting spatula in place, until the blood pressure became constant again. When after this we obtained a rise of blood pressure on electrically stimulating the oculomotor nerve, we were completely convinced that the rise is mainly, if not wholly, due to this stimulus rather than to any other complicating factor.

We give here the results obtained in one of the three experiments which we have successfully performed. At first the oculomotor nerve was stimulated with an appropriate faradic current. There was a rise of blood pressure of about 50 mm. of Hg (Fig. 1).

The fourth nerve was then stimulated with the same strength of current, and a rise of blood pressure of about 40 mm. of Hg was obtained (Fig. 2).

It is to be noted, however, that these two stimulations were applied to the intact nerves just before they enter the cavernous sinus. It was impossible to ligature the nerve and hold it with a thread during stimulation, first because the location of the nerves does not easily allow such manipulation, and secondly because their intradural part is very poor in perineural connective tissue, and so withstands no ligature of any kind.

The left cerebral hemisphere was then removed. A rest of 10 min. was allowed before we attempted any further stimulation. The central ends of both

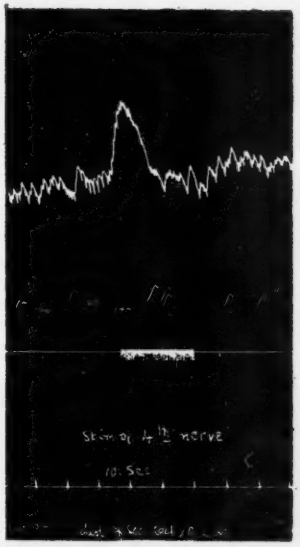

Fig. 2. A tracing which indicates a rise of blood pressure of the same dog of about 40 mm. of Hg on intradurally stimulating the trochlear nerve as it leaves the brain stem.

nerves were stimulated again as before, a rise of blood pressure about 32·8 mm. of Hg was obtained in the case of the third nerve (Fig. 3), and in the case of the fourth the rise was 31 mm. of Hg (Fig. 4).

The central cut ends of both nerves were then mechanically stimulated with a pair of forceps; a rise of blood pressure was recorded in both cases. The rise was about 10 mm. of Hg in the case of the oculomotor (Fig. 5) and about 8·9 mm. of Hg in the case of the trochlear (Fig. 6). This rise, due to mechanical stimulation, proves beyond doubt that the rise obtained during electrical stimulation was not due to any spread of impulse to the surrounding structures, but to the stimulation of sensory fibres in the trunk of the stimulated nerve.

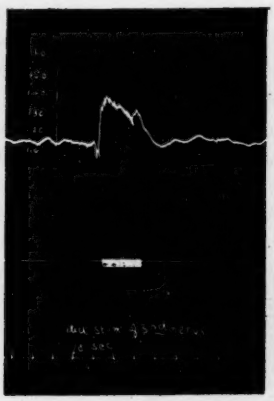

Fig. 3.

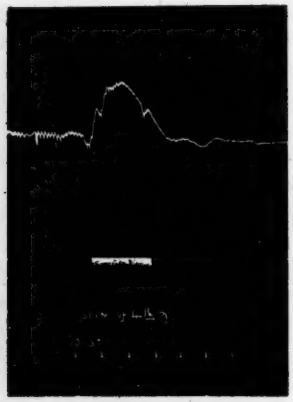

Fig. 4.

Fig. 3. The result of the electrical stimulation of the central end of the oculomotor nerve, after removal of the corresponding cerebral hemisphere. The rise was about 32·8 mm. of Hg.

Fig. 4. A record of electrical stimulation of the central end of the trochlear nerve under same conditions as in Fig. 3 produced a rise of about 31 mm. of Hg.

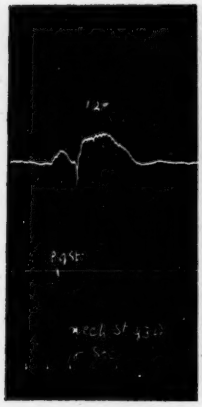

Fig. 5.

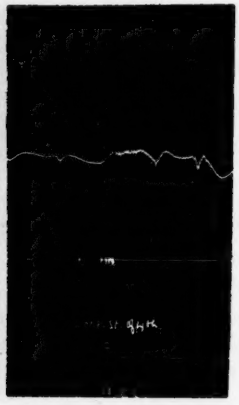

Fig. 6.

Fig. 5. A tracing of the rise of the blood pressure about 10 mm. of Hg produced by the mechanical stimulation of the central end of the oculomotor nerve intradurally.

Fig. 6. The same was applied to the trochlear nerve under the same conditions giving a rise of blood pressure of about 8·9 mm. of Hg.

We have managed to approach the sixth nerve after removal of the right cerebral hemisphere, and we were able in one of our experiments to record a rise in the blood pressure of the animal after both electrical and mechanical stimulations of the central end of this nerve (Fig. VII*a*, *b*).

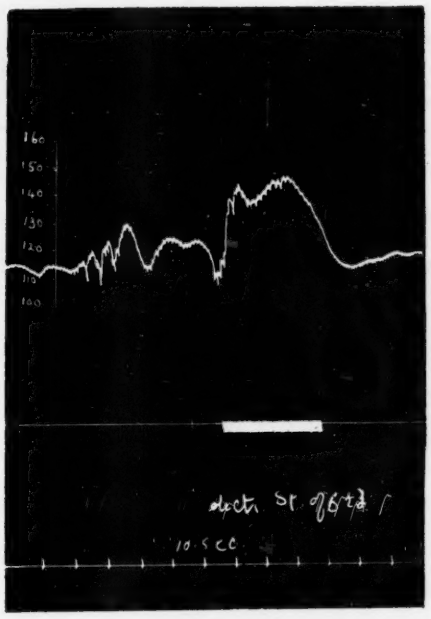

Fig. 7*a*.

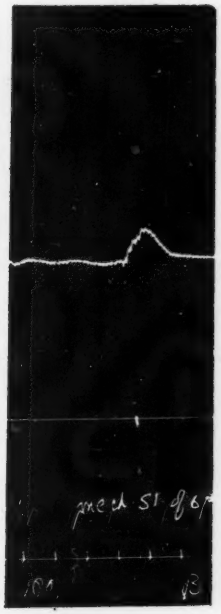

Fig. 7*b*.

Fig. 7. The result of (*a*) electrical, and (*b*) mechanical stimulations of the central end of the abducent nerve.

Neither electrical nor mechanical stimulation of the peripheral ends of any of these nerves resulted in any change in the blood pressure of the animal under exactly the same conditions.

CONCLUSIONS

It is, therefore, right to conclude that the third, fourth, and sixth cranial nerves emerge from the brain with sensory fibres already incorporated in their nerve trunks.

We believe, therefore, that by these experiments we obtained further evidence of the sensori-motor nature of the ocular nerves, as has been pointed out by Sherrington & Tozer, and later by others.

I wish to thank my chief, Prof. Dr D. E. Derry, for his kind interest and encouragement, and Prof. G. von Anrep for permitting me to work in his Department, as well as for his criticism. My thanks are also due to Dr A. A. Tarkhan at whose suggestion this work was done, to Dr H. Kashif and A. Fargally for their kind help during the experiments.

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THE INNERVATION OF THE HUMAN GUM

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The innervation of the human gum is a subject which has received relatively little attention. Jurjewa (1913), published an elaborate account of the nerve endings of this region and described a very large number of different types. Kadanoff (1928), in an excellent paper, criticizes Jurjewa's work in that it is impossible from his description to determine whether these nerve endings are found in the human gum or whether some of them only occur in the gums of other animals, and Kadanoff in Man was unable to find several of these nerve endings. Kokubun (1929) gave an account of the innervation of the human gum which differs little from that of Kadanoff, except that he describes the presence of cells of Langerhans. No other worker mentions the presence of such cells in this tissue, and we ourselves have not been able to see them. The papers of all these investigators were illustrated by line drawings and, although these are very clear, they suffer from the disadvantage that it is not easy to compare their results with one's own. For such a purpose, photomicrographs are much more satisfactory. So far as we have been able to discover, the only investigators who have published photomicrographs are Hosaka (1936) and Mowry (1930). The former, although he demonstrated nerve endings, had photomicrographs which are technically unsatisfactory. Mowry presents one or two photomicrographs of the intra-epithelial course of the nerve fibres, but he does not discuss the innervation of the gum.

In this present investigation we have followed the lines adopted in our previous work on the periodontal membrane. The material was obtained from the living patient by snipping off tags of gum immediately after the extraction of teeth. Unfortunately, no note was taken of the site from which these specimens came, so that we are unable to give any opinion as to the position of the different endings about to be described. The specimens were immediately placed into ammoniated alcohol, and were then stained by the modification of Cajal which has been devised by Gooding & Stewart (1937). The value of this method is that it prevents, to a great extent, precipitation of the silver in the other tissues. After the staining was complete, the specimens were embedded in paraffin and serial sections were cut. The results were very satisfactory and there was no difficulty in obtaining photomicrographs.

From a study of the literature, we have come to the definite conclusion that by far the best account is that of Kadanoff and, in this communication, we shall discuss his findings and compare them with our own. This author divides up the end-organs into those which are capsulated and those which are non-encapsulated. The capsulated endings are of two types, end-bulbs and

touch corpuscles. The end-bulbs are of the Krause type and are found in two situations, those deep down in the connective tissue and those in the papilla. Nothing will be said about the deep ones, as this investigation has been confined to the nerve endings in the papillae and the epithelium.

In regard to the end-bulbs found in the papilla, Kadanoff states that one and sometimes two nerve fibres enter the capsule. Within the capsule, the fibre divides into branches, and these further subdivide and finally coil round and anastomose with each other to form a remarkably closed coil. Kadanoff is of the opinion that these branches do not have free endings. He was unable to find any other structure within the end-bulb. The touch corpuscles, which he describes as Meissner bodies, differ little from the others except that cells are actually present within the corpuscle.

The present authors could not detect any definite capsules around the bodies, nor have they been able to establish any particular relation between the cells and the end-organ and, therefore, have been unable to differentiate between the two types. For this reason, Kadanoff's encapsulated organs will be discussed together. Numerous examples of these end-coils have been observed in the present investigation, and from a study of them it is quite clear that, in certain points, they vary from the description given by Kadanoff. Many more than two fibres may run into the organ to form it. No branching of these nerve fibres has been seen, and the authors believe that they simply coil round each other to form the end-bulb. One of these end-bulbs is shown in Pl. I, fig. 1. This consists of three photomicrographs from adjoining sections, and demonstrates clearly that several nerve fibres are taking part in the formation of the end-bulbs and that they do not branch or divide. It is interesting to note that, in some of Kadanoff's drawings, there is no sign of any branching of the nerve fibres which form these structures. Kadanoff was unable to find that any nerve fibres pass from this coil to the epithelium, and our work confirms that observation.

Kadanoff divided the non-encapsulated fibres into three types, close coils, loose coils and free endings. According to that author, the close coils have a similar structure to the encapsulated coils already described, but are smaller. The nerve fibre divides into two or three branches on entering the coil and these branches twist upon each other. From the coil thus formed branches arose, some of which ran out to the epithelium. We have seen several examples of this type of coil during this investigation, and agree with much of what Kadanoff says about these structures. However, as in the case of the encapsulated endings, the nerve forming the organ does not branch, and the structure is formed simply by the fibre coiling upon itself. The intra-epithelial nerve fibres which arise from this coil are much thicker than those which come from other sources, and have a less wavy course in the epithelium. In Pl. I, fig. 2, an example of one of these end-coils is illustrated with a thick intra-epithelial fibre arising from it. Unfortunately, the superficial layers of the epithelium have been torn away so that the fibre cannot be traced to its termination. In

Pl. I, fig. 3, however, although the coil itself is only partially seen, the intra-epithelial fibre can be followed throughout its course, to end a short distance from the surface in a definite thickening.

Kadanoff's loose coils were formed by one or more nerve fibres entering the papilla from the subpapillary layer. These fibres gave off branches which formed a loose network occupying a large part of the dome of the papilla. He was unable to determine whether the network was a close one or not, but his illustrations suggest that it is. From this loose coil fibres were given off which passed to the epithelium. Similar structures have been found during the present research, and correspond completely with the findings of Kadanoff. In thin sections, such as Pl. II, fig. 4, it is, of course, impossible to see the whole of the coil so that, in this photomicrograph, only a part of it is visible. An intra-epithelial fibre arising from the loose papillary network is, however, present and it is much thinner than the fibres which arose from the tight coils in Figs. 2 and 3. These thin fibres have a wavy course in the epithelium, and many of them end in a small rounded swelling.

Pl. II, drawing 1, is a reconstruction from another specimen, and the fine intra-epithelial fibres will again be noticed. In this example some of these fibres branch, but the branching is much less marked than would be expected from the descriptions in the text-books of the normal course and distribution of intra-epithelial fibres.

Kadanoff mentions a third source of intra-epithelial fibres, namely, a fine network lying alongside the cells lining the papilla. Such a network has not been found during this investigation. Its place appears to be taken by a single nerve fibre lying directly below the epithelium, which at intervals is reinforced by nerve fibres in the form of a loop. This structure is illustrated in Pl. II, drawing 2, built up from six consecutive sections.

It will be observed that the infra-epithelial nerve supplies numerous thin intra-epithelial fibres which are similar to those which arise from the papillary network. Their course is wavy and they tend to branch. They often end in small knob-like swellings. The relations of these endings to the epithelial cells is of some interest, but our sections are too thick to permit us to say whether their terminations are within the cells, but they seem to be closely related to them (Pl. II, fig. 5).

The nerve loops which strengthen the infra-epithelial nerves have already been mentioned, and one of these is present in Pl. II, fig. 6.

Kadanoff believes that the epithelium of the gum, as a whole, has a rich nerve supply. This, however, only occurs in certain regions, and in others we have been unable to detect any intra-epithelial fibres and, as the nerve fibres were quite clearly stained in other parts in the sections, we do not consider that the lack of nerve fibres in these regions is due to errors of technique.

From his material, Kadanoff was able to state that the various types of nerve endings which he describes are localized in particular regions of the gum. It has already been stated that, unfortunately, we took no account of

the localities from which our specimens were removed, but what evidence we have tends to confirm Kadanoff's conclusions, as some of these specimens show only one type of nerve ending, and others show another.

SUMMARY

The following types of nerve endings were found in the gum:

1. Close coils located near the apices of the papillae. There were two varieties of these:

(*a*) Large, the fibres forming which did not branch but simply twisted and coiled upon each other.

(*b*) Small, from which originated a thick intra-epithelial fibre.

2. Loose coils or networks, occupying the whole of the papilla. Fibres forming these coils branch, and from the coils arose fine intra-epithelial fibres.

A further group of fine epithelial fibres arose from a subepithelial nerve which was reinforced at intervals by nerve loops. The fine epithelial fibres had a much more wavy course than the thick ones which arose from the small close coils.

ACKNOWLEDGEMENTS

Thanks are due to Prof. Stopford for facilities for carrying out this investigation in the Anatomy Department of the Victoria University, Manchester. We are greatly indebted to Mr Gooding for the preparation of the specimens and to Mrs Lewinsky who has kindly drawn the reconstructions.

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EXPLANATION OF PLATES I AND II

Plate I

Fig. 1. Photomicrograph of three adjoining sections to show the formation and structure of a large close coil.

Fig. 2. Small close coil giving origin to thick intra-epithelial fibre. The surface layers of the epithelium have been torn away.

Fig. 3. Thick intra-epithelial fibre arising from a close coil. The latter is not clearly shown in the specimen.

Plate II

Fig. 4. A loose coil.

Fig. 5. Nerve loop giving off thin intra-epithelial fibre. The course of the latter is interrupted.

Fig. 6. Thin intra-epithelial fibre.

Drawing 1. Reconstruction of loose coil and fine intra-epithelial fibre.

Drawing 2. Subepithelial nerve giving origin to numerous intra-epithelial fibres.

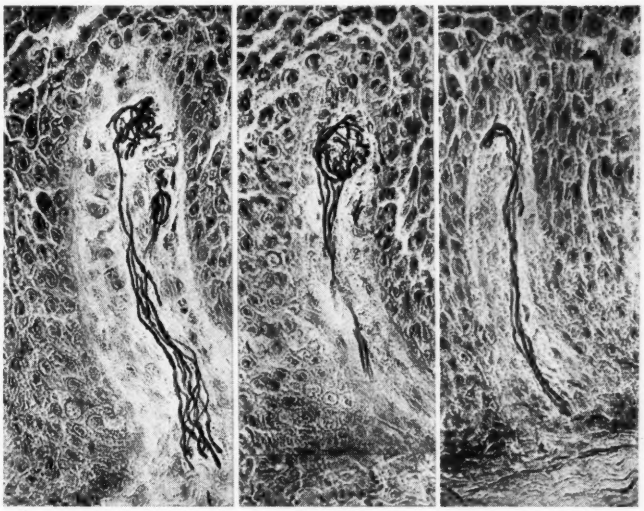


Fig. 1.

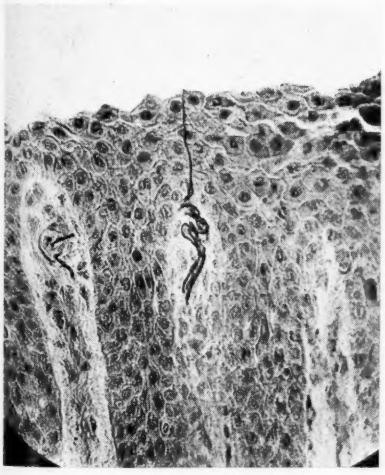
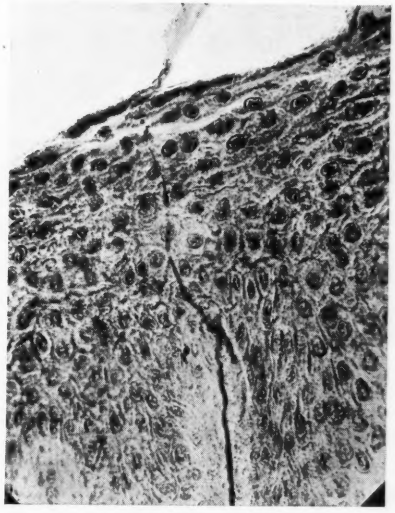


Fig. 2.



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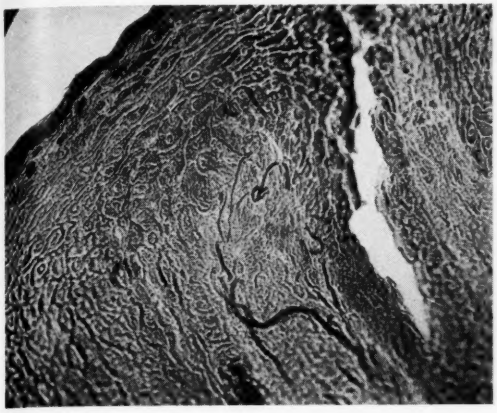
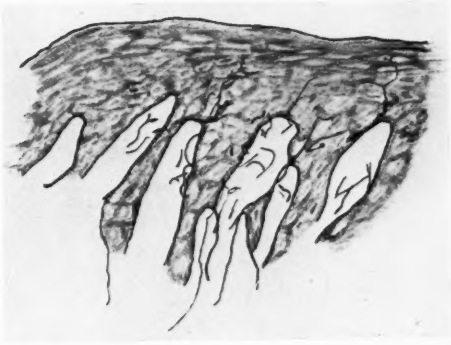


Fig. 4.

Fig. 5.



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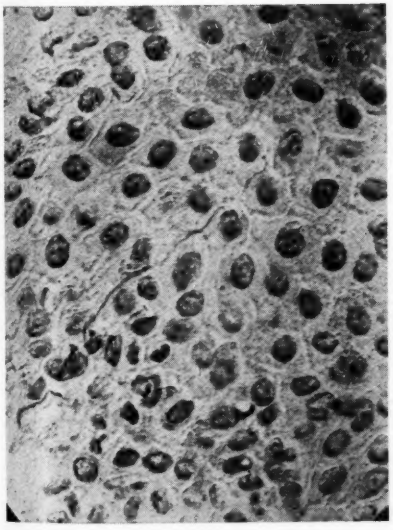

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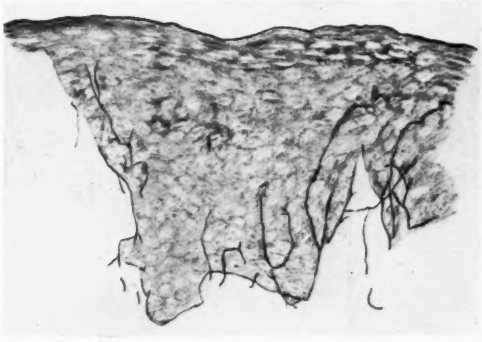

Drawing 2.

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THE EXTERNAL MORPHOLOGY OF THE BRAIN OF *TESTUDO GEOMETRICA*

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INTRODUCTORY

In the present paper I have aimed at supplying a brief account of the external morphology of the brain of *Testudo geometrica*. During the past few years I have also been concerned with the investigation of the cell masses, the fibre tracts and the blood vessels of this brain. As the latter work has already been completed, it is possible to include here a description of only such features as are relevant, and which will serve as a topographical guide in connexion with the other sections of this study. Their importance as anatomical landmarks will, however, be more appropriately considered in connexion with the studies of the cell masses, fibre tracts and blood vessels of the brain.

MATERIAL AND METHODS

Several species of the South African land tortoise were available for examination, and during the course of the investigation a considerable number of brains were studied. But the species *T. geometrica*, which was obtained from East Bechuanaland, was the most abundant, and for the sake of uniformity only this species will be considered in the present account. In order to identify the various types, a classification of the South African Chelonidae suggested by Fitzsimons was put at my disposal by Mr Pringle of the Port Elizabeth Museum.

The brains were for the most part studied directly by means of the binocular microscope. But where difficulties were encountered reconstructions were prepared on graph paper, by mapping the contours of various aspects from serially sectioned brains. In preparing these reconstructions the following variations from the technique ordinarily used in this department (Dart, 1934) were used: (*a*) In mapping the contours of the dorsal and ventral aspects, the co-ordinate measurements were not taken from the medial margins of the hemispheres, or optic lobes, which Dart represents as a straight line coinciding with the linear abscissa. The linear abscissa represented the sagittal midline of the brain; and the contours of its medial margin were thus also determined, thereby avoiding much distortion. (*b*) In the case of the projection maps of the lateral and the medial aspects, very gross distortion of the shape of the brain is introduced in those prepared by Dart when the dorsal margin of the brain was regarded as a straight line. The following technique was thus devised:

A large piece of human liver was fixed in 10 % formalin. After being well hardened it was cut into rectangular slabs of about $3 \times 1 \times 0{\cdot}5$ cm. Each such slab was dehydrated and embedded in paraffin. One flat surface was then trimmed smooth with the microtome, but the slab was not planed thin yet, for it was discovered that subsequent re-embedding tended to warp it, if this were done. When the brains were ready to be embedded, each was placed on its dorsal aspect on the planed surface of the liver slab, which had meanwhile been melted out of its block and placed, smooth surface uppermost, in the container for the new block. When this new block, containing the liver slab and the brain in correct apposition, had hardened sufficiently, the rough surface of the liver slab was trimmed smooth on the microtome. It was planed away in this manner until about 1 mm. in thickness. The block was then ready for serial sectioning. It was found to be better if the microtome knife cut the liver before cutting the brain. In mounting the serial sections the utmost care was taken to retain the original relationship between the liver strip and the brain tissue. Thus a serially sectioned brain was mounted in one sitting. The temperatures of the oven, the amount of water placed on the slide, etc., were kept as constant as possible; and the wax was allowed to expand evenly for exactly the same time in the case of each slide.

By the introduction of these two modifications most of the distortion of the cartographic reconstructions was avoided. A further source of possible distortion in these projection maps is the fact that any inclination of the plane of sectioning, other than at right angles to the planed surface of the liver strip, causes the sections to appear larger than they should be. While examining the range of such distortion under varying inclinations of the plane of sectioning, the avoidance of this error was found to be a considerably easier matter than its subsequent mathematical correction.

To obtain accuracy of pictographic representation, a micrometer-grid was inserted into the dissecting microscope ocular and the external morphology of the brain then drawn to scale on graph paper. Comparison with the cartographic reconstruction described above made it possible to prepare the sketches which accompany this description (Figs. 1–6).

DESCRIPTION AND DISCUSSION

The brain

Though belonging to a uniform species, the brains varied considerably in size (e.g. 10–20 mm. in length). This variation was not in direct proportion to the bulk of the animal, as very small tortoises were observed to have relatively large brains. The very heavy carapace of the animal, however, inclines one to the conclusion that the *index of cephalization* (*vide* Kappers, 1929) is not applicable in this instance. Data for *T. geometrica* are therefore not included in this account.

Regarding the meninges little need be said. Although the larger venous sinuses of the endocranial blood vascular system are closely related to the

strong, thick dura mater, which is firmly adherent to the skull bones only in the older specimens, nothing comparable to the sagittal sinus of mammals was found. The majority of the blood vessels of the brain lie in the limited interval

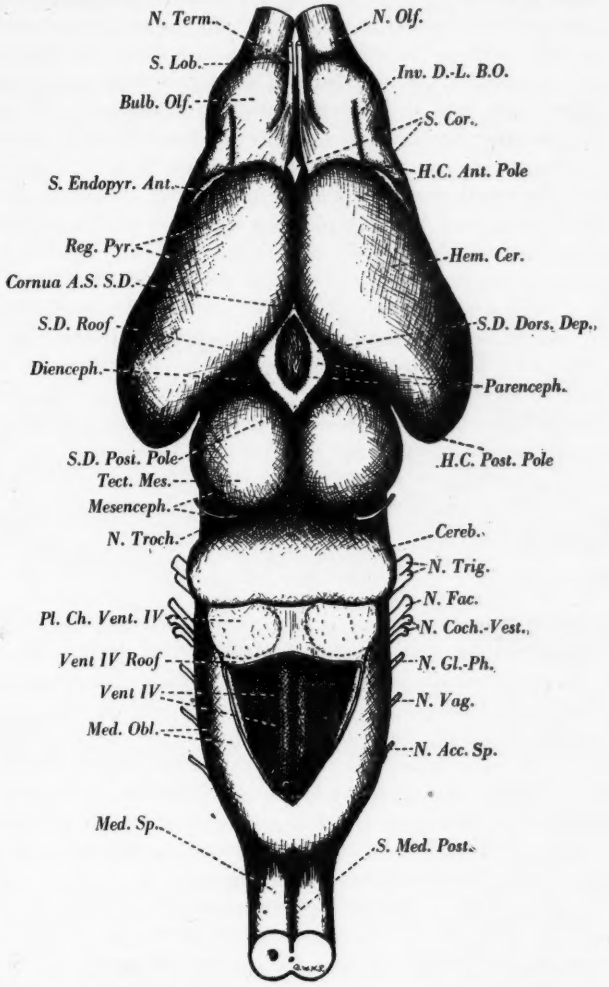

Fig. 1. The dorsal aspect of the brain of *Testudo geometrica*. (10 × natural size.)

between the delicate pia mater and the dura, which represents the arachnoid tissue (Kappers, 1929).

The general proportions of the brain are evident from the sketch of the dorsal aspect (Fig. 1). The hemispheres (*Hem. Cer.*) are the largest structures,

but they seem relatively short because they are so orientated that their long axes are not parallel to one another as in *Chelone midas* (De Lange, 1911), and their posterior poles, like those of *Cistudo carolina* (Johnston, 1915), are widely separated and thus embrace not only the dorsal sac and epiphysial structures, but also the anterior half of the optic tectum, as in *Chelone midas*. These differences may perhaps be correlated with the fact that the optic lobes (*Tect. Mes.*) themselves are rounded and proportionately larger than in the chelone where they tend to be anteroposteriorly flattened. The cerebellum (*Cereb.*), on the other hand, is considerably smaller in *Testudo geometrica*. In the chelone the cerebellum, which is convex upwards, overhangs practically the whole of the fourth ventricle (Elliot Smith, 1902; De Lange, 1911); but in *T. geometrica*, as is more or less typical for the non-swimming reptiles, it is a mere vertical plate which is slightly convex anteriorly and concave posteriorly and whose lateral margins may be everted, as in Fig. 2 (*Ev. E. Cer.*). Practically the whole of the fourth ventricle (*Vent. IV*) is thus left exposed to view from the dorsal aspect, so that the large masses of choroid tissue on each side (*Pl. Ch. Vent. IV*) can be distinguished behind the cerebellar fold, where they project into the fourth ventricle.

One hardly hesitates to correlate the smallness of the cerebellum and the greater size of the optic tectum and cerebral hemispheres with the significance of vision and other sensations and the relative unimportance of equilibration and kinaesthetic sensations in the terrestrial *T. geometrica* as compared with the aquatic chelones.

The cerebral hemispheres

From the dorsal aspect (Fig. 1) the cerebral hemispheres are seen to be roughly oval in outline, with a slight angulation of the medial contours, where these of the two opposite sides diverge after being closely applied to one another anteriorly. Where a branch of the middle cerebral artery crosses over on to the dorsal aspect, the lateral contour on both sides shows a slight indentation. In most brains the sulcus coronalis (Unger, 1906) or sulcus olfactorius (Kappers, 1921), which demarcates the olfactory bulb from the anterior pole of the hemisphere (*S. Cor.*), is shallow. In others, however, this sulcus is deep and is associated with a forward projection of the anterior pole (*H.C. Ant. Pole*) as in the chelone (Johnston, 1915).

The dorsal surface of the hemisphere tends to be flattened. Some such flattening here seems to be characteristic of the brains of the Chelonia in general, especially the land types, but is exaggerated in the case of the South African tortoise. In spite of this relative flattening of the dorsal surface no sulcus is found there which corresponds to the "sulcus longitudinalis" of the Varanidae (De Lange, 1911).

The olfactory bulbs (*Bulb. Olf.*), though sessile, as is typical of Chelonia, are elongated, and, by increasing steadily in width from before backward, pass over into the ill-defined olfactory lobes of the hemisphere. Laterally, about their

middle, they have a shallow elongated groove, and at their anterior ends they are, as seems to occur generally in the chelone, sharply delimited from the olfactory nerves by the "sulcus lobaris" (De Lange, 1911) (Figs. 1–4; *S. Lob.*). Medially, opposite the anterior poles of the hemispheres there is a rhomboid interval between the bulbs, where the sulcus coronalis or olfactorius continues on to the medial aspect.

An important feature of the dorsolateral aspect of the olfactory bulb (Figs. 1 and 2) is the occurrence of a slight fissure, or, more accurately, invagination (*Inv. D.-L. B.O.*), at the junction of the upper third and lower two-thirds and opposite the region of transition from olfactory bulb to the olfactory lobe of the hemisphere. This has been termed the "dorsolateral bulbar invagination". Such an arrangement has not yet been described in

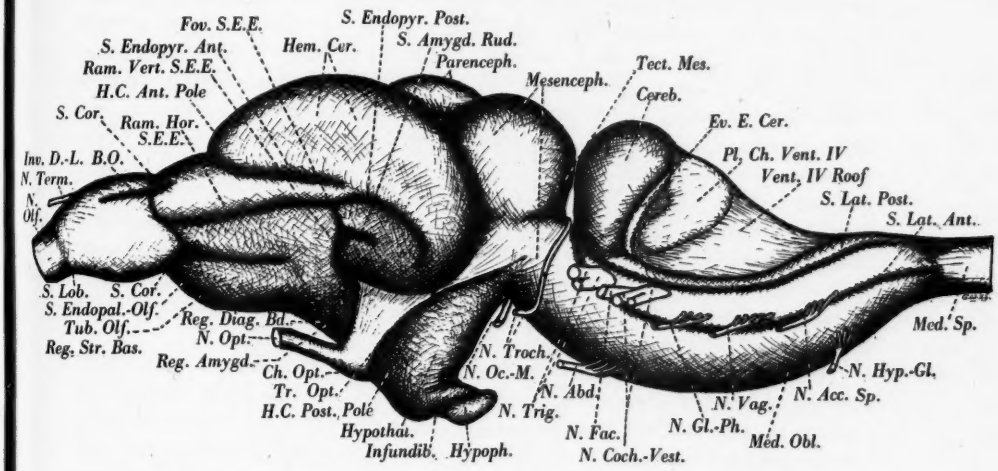

Fig. 2. The lateral aspect of the brain of *Testudo geometrica*. (10 × natural size.)

Reptilia. Elliot Smith, however, as long ago as 1894, described a similar, though certainly more obvious and deeper invagination of the lateral wall of the olfactory bulb in *Ornithorhyncus*, and also later (1898) in the Edentate *Orycteropus*. In his case "complete fissures" were present, but he did not explain or discuss their significance at any length.

The sulci of the external aspect

The external endorhinal sulcus, with its horizontal (*Ram. Hor. S.E.E.*) and vertical (*Ram. Vert. S.E.E.*) branches, set nearly at right angles to each other at the fovea endorhinalis (*Fov. S.E.E.*), lies across the lateral aspect of the hemisphere at about its middle (Fig. 2). Whereas the vertical limb is deep, being described by De Lange as an "Einkerbung", the horizontal portion is shallow, as is generally the condition in reptiles. Two

sulci pass backward from the vertical limb. The lower of these (*S. Amygd. Rud.*), which may be quite deep and distinct, but is generally rather inconspicuous, arises from the vertical limb near its inferior termination (Fig. 2) and extends horizontally backward for some distance. In view of its relationship to internal cell formations, it is a rudimentary amygdaloid fissure comparable to that fissure in *Cistudo carolina* (Johnston, 1915). It is evidently also homologous with the posterior half of the endorhinal sulcus in *Lacerta viridis*, which is described by Goldby (1934) as a single horizontal groove with no separate horizontal or vertical limbs.

The upper of these two posterior branches of the vertical limb is directed obliquely upward and backward and arises from the endorhinal sulcus at the junction of the horizontal and vertical limbs. Though it is less distinct than the lower one, it extends across the pyriform lobe for some distance and terminates by becoming continuous with a second shallow but better defined groove (*S. Endopyr. Post.*), which is directed downward and backward, ending some distance from the posterior pole of the hemisphere after curving sharply downward following more or less the contour of the hemisphere (Fig. 2). As this important sulcus has not been described before, it will, on account of its relation to the pyriform cortex, be spoken of as the posterior endopyriform sulcus.

The horizontal limb of the endorhinal sulcus fades out in the region of the sulcus coronalis anteriorly. It is nearly in line with the posterior endopyriform sulcus just described. The two should, however, be carefully distinguished, as they have not the same topographical significance with regard to the internal structure of the hemisphere.

In the angle between the horizontal and the vertical limbs of the endorhinal sulcus, across a depressed flattened area representing the basal striatal cell masses (Figs. 2 and 3) a shallow sulcus (*S. Endopal.-Olf.*) extends horizontally backward from the sulcus coronalis anteriorly till near the vertical limb of the endorhinal sulcus, where it disappears. As it corresponds to a line of separation of the tuberculum olfactorium (*Tub. Olf.*) or palaeo-olfactory cortex (Dart, 1925) into dorsal and ventral zones, it may be referred to as the endopalaeo-olfactory sulcus. It is an important channel along which run the veins which drain these basal regions.

Finally, there may also be distinguished on the dorsolateral aspect, just above the horizontal limb of the endorhinal sulcus (Figs. 1 and 2), a groove (*S. Endopyr. Ant.*) which sweeps backward from the region of the coronal sulcus, so that it gradually approaches the horizontal branch of the endorhinal sulcus. It fades out where the latter meets the vertical limb. A sulcus, corresponding morphologically to this one, has been described in the case of the brain of *Chelone midas* by Elliot Smith (1919), who, owing to its position on the lateral surface of the hemisphere and its lateral relationship to his primordium neopallii, did not hesitate in homologizing it with the fissura rhinalis of lower mammals, which has an identical situation (cf. Kappers, 1921).

Whether this sulcus is actually homologous with the primitive marginal sulcus of the mammal is uncertain. Its relationship to the pyriform pallial formations is, in *Testudo geometrica*, almost similar to that of the posterior endopyriform sulcus, and it will therefore be referred to as the anterior endopyriform sulcus.

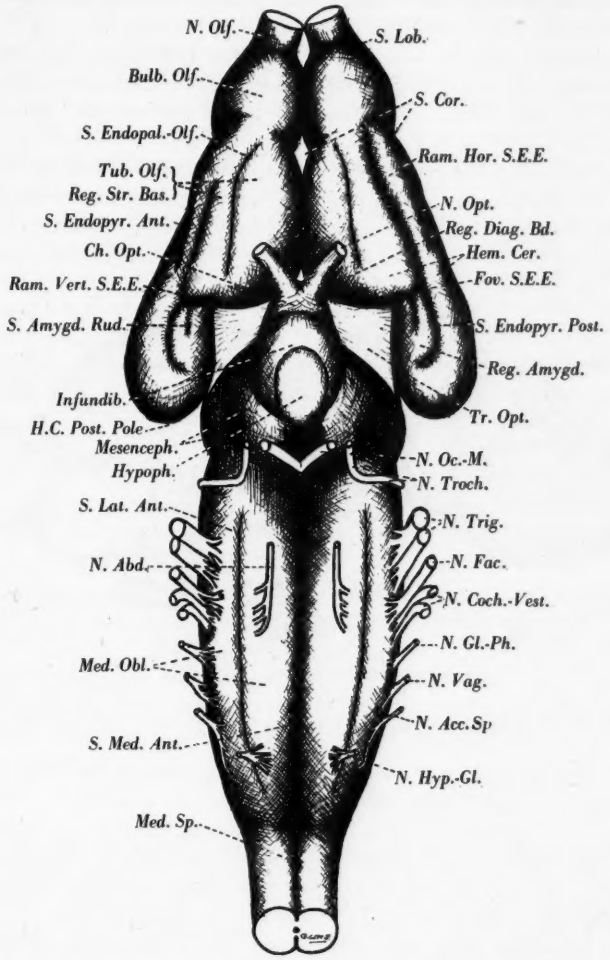

Fig. 3. The ventral aspect of the brain of *Testudo geometrica*. (10 × natural size.)

The medial surfaces of the hemispheres (Fig. 4) are flattened over the areas where they are applied against one another. Opposite the junction of the lower two-thirds and upper third of the medial surface of the olfactory bulb the nervus terminalis (Johnston, 1913*a*; Herrick, 1921) was conspicuous in

several instances. As represented in Figs. 1 and 4 (*N. Term.*) it is seen to be quite separate from the olfactory nerve (*N. Olf.*), and, after becoming flattened out, to terminate over the dorsomedial aspect of the region of transition from the olfactory bulb to the olfactory lobe of the hemisphere.

No structure comparable to the accessory olfactory bulb, recently stated to occur in *Lacerta viridis* (Goldby, 1934), could be discerned.

The olfactory bulb is demarcated from the hemispheres by two nearly vertical shallow sulci meeting at an obtuse angle to each other opposite the middle of the lobe. These are the medial ends of the coronal sulcus (*S. Cor.*) which was seen in Figs. 1, 2 and 3.

From the angle made between these two medial ends a sulcus (*S. Sept.-Cort.*) runs directly backward to lead into the upper anterior corner of the interventricular foramen (Figs. 4 and 5). Though on first appearances it may seem to correspond to the much discussed fimbrio-dentate sulcus of Johnston, its

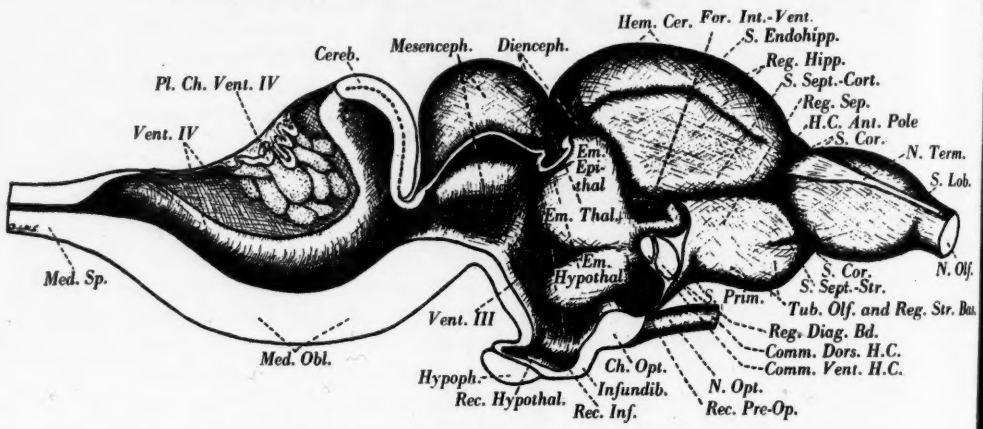

Fig. 4. The medial aspect of the brain of *Testudo geometrica*. (10 × natural size.)

cell mass relations prove it to be more directly comparable with the sulcus limitans hippocampi of Elliot Smith (1899) and the sulcus septo-corticalis of De Lange (1911), and of Kappers (1921). It is important to note that, though it meets the interventricular foramen at its superior anterior corner, it is not continued backward over the interventricular foramen into the posterior pole of the hemisphere, as is the equivalent sulcus in other reptiles.

There are three more sulci which may be distinguished on the medial surface of the hemisphere in this brain (Fig. 4). Two lie below the sulcus just described, i.e. in the septal region. The remaining one is above this sulcus, i.e. in the hippocampal region. Of the lower two, one (*S. Sept.-Str.*) appears to be a branch of the ventral end of the coronal sulcus, and passes horizontally backward for a short distance. Being coincident with the lower margin of the septal or par-olfactory nucleus (or the paraterminal body), where it lies next

to a medial portion of the palaeostriatal basal cell mass not covered with tuberculum olfactorium (or palaeo-olfactory cortex), this sulcus is a valuable landmark. As it is generally not a very obvious feature of the reptilian brain, it appears to have been recognized only once before, when it was called the sulcus rhinalis medialis (Johnston, 1913 *b*). This name is misleading and has been previously criticized. It will here be referred to as the septo-striate sulcus.

The other of these two lower sulci is the sulcus primus. It commences on the ventral aspect of the brain, but is obscured from view by the optic nerves in Fig. 3, and is first seen in Figs. 4 and 5 (*S. Prim.*) where it curves upward in front of the lamina terminalis (*Lam. Inf.-N.-P.*) and some distance in front of it. It lies opposite the anterior margin of the diagonal band of Broca (*Reg. Diag. Bd.*).

The remaining sulcus of the medial aspect (*S. Endohipp.*), which lies opposite the hippocampal cortex near its dorsal margin, is long and tortuous and is distributed over the whole length of the medial surface (Fig. 4). Corresponding to a line of separation of the hippocampal cortex into two distinct cell formations or zones it should be regarded as a limiting sulcus. For the present purpose it will be referred to as the endohippocampal sulcus, as it cannot at this stage be definitely homologized with any of the sulci so far described for Reptilia. It might possibly correspond to the sulcus longitudinalis (De Lange, 1911), whose presence has been demonstrated along the medial edge of the dorsal surface of the hemispheres in other reptiles.

The posterior portion of the medial surface of the hemisphere is obscured from view by the diencephalon and also by the optic tectum in Fig. 4. On removal of these it is seen to be slightly concave over its whole extent and to face backward and downward as well as medially. The endohippocampal sulcus may be traced further over this part of the medial surface. It is seen to follow the dorsal contour of the hemisphere fairly closely, curving backward and downward towards the posterior pole of the hemisphere. From here it continues downward and forward, again following the contour of the hemisphere. It terminates near the tapering posterior end of the interventricular foramen.

The commissures

The anterior commissure or ventral commissure (*Comm. Vent. H.C.*) and the combined anterior pallial and hippocampal commissures (*Comm. Dors. H.C.*) or dorsal commissure (Elliot Smith, 1899), though very small, are yet easily defined from one another (Figs. 4 and 5). The dorsal commissure (*Comm. Dors. H.C.*) is the larger of the two and is in this case most anteriorly situated. It is broader inferiorly than superiorly, and its upper end is on a level with that of the ventral commissure, while its lower end extends much farther down. It is concave on its posterior aspect, where the convex anterior surface of the ventral commissure lies against it. Its anterior surface is convex forward. The ventral commissure (*Comm. Vent. H.C.*) is oval in cross-section.

Its fibres can be seen to pass laterally and slightly downward. The fibres from the lower part of the dorsal commissure are directed mainly forward and upward at their commencement, whereas those from the superior end continue backward and upward, not unlike the fornix of lower mammals (Elliot Smith, 1902,

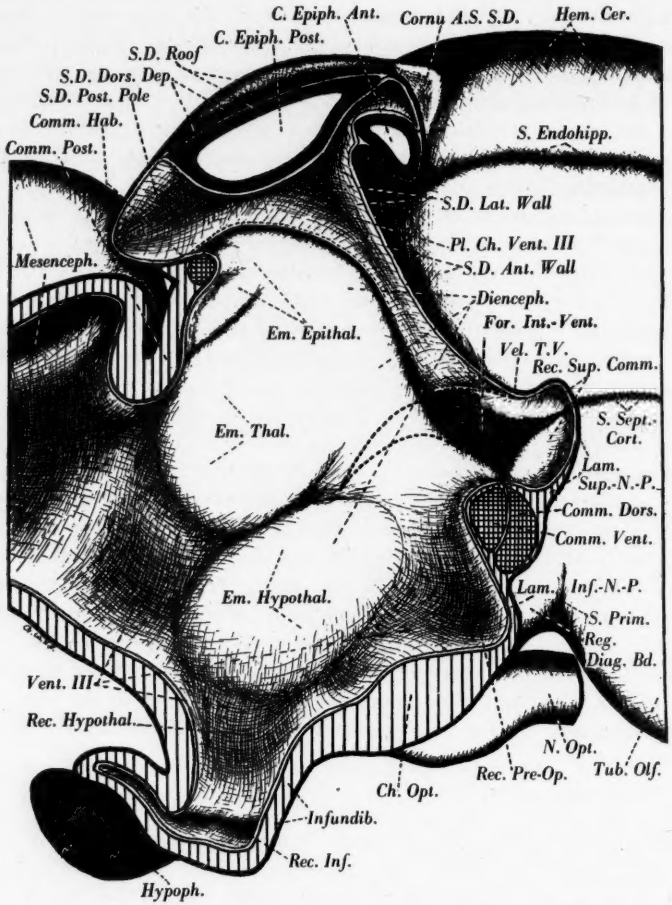

Fig. 5. A reconstruction of the structures of the medial aspect of the diencephalic region of the brain of *Testudo geometrica*. (40 × natural size.)

It is at once obvious that, as compared with the condition in some other reptiles such as *Cistudo carolina* and *Chelone midas* (Johnston, 1913*b*) and in the Selachian and embryonic reptilian brain, these two commissures have been approximated; indeed, the dorsal commissure has come to lie in

front of or even slightly lower than the anterior commissure. The anterior neuroporic recess, which Johnston maintains is always situated above the ventral commissure, has thus in this instance been completely obliterated, and the expanded lower end of the lamina supra-neuroporica (*Lam. Sup.-N.P.*) of Burckhardt (1894), in which the dorsal commissure is embedded, has become fused with the expanded upper end of the lamina infra-neuroporica (*Lam. Inf.-N.-P.*) (which is equivalent to the lamina terminalis of Johnston (1913*b*)), in the posterior portion of which lies the ventral commissure (Figs. 4 and 5).

The ependymal recesses

The third ventricle, which is exposed in a median sagittal section (as in Figs. 4 and 5), has several ependymal recesses of importance. That formed between the optic chiasma below and the commissures above is the pre-optic recess (*Rec. Pre-Op.*). Its lateral wall consists of an area, limited behind by the hypothalamic eminence (*Em. Hypothal.*), which corresponds to the location of the pre-optic nucleus.

There is another recess, the supracommissural recess, which lies in front of the interventricular foramen, and which is bounded inferiorly by the dorsal commissure and anteriorly and superiorly by the lamina supra-neuroporica (Figs. 4 and 5, *Rec. Sup.-Comm.*). It is obviously comparable with the supra-commissural diverticulum of the third ventricle, described by Elliot Smith (1899) in *Ornithorhyncus*, which he regards as a distinctly saurian feature of that brain, though it is actually an even more primitive structure. He also referred to it as the recessus dorsalis. Similar recesses have been mentioned by Johnston (1923), Gisi (1907) and others.

This supracommissural recess, while closely related to the paraphysis of the primitive vertebrate brain, should yet not be confused with it, even though many authors regard any recess anteriorly to the velum transversum as being paraphysis. It resembles more directly the recessus superior of the embryonic domestic fowl (v. Hallerstein, 1934), for it is truly a recess consisting of un-specialized ependyma and pia mater. In the embryonic domestic fowl the true paraphysis lies immediately posterior to the recessus superior. Its walls are thickened and glandular, as in other more primitive forms. Frazer (1931) and other authors claim that the paraphysis is originally a stalked, vesicular, glandular and perhaps paired organ. They do not distinguish clearly enough, however, between the true and specialized paraphysis and the ependymal recess, which is bounded posteriorly by the velum transversum and anteriorly by the lamina supra-neuroporica, and which is characteristically present in *Petromyzon* (though Kappers designates it here as paraphysis), and persists in such reptilian forms as the Chelonia. The supracommissural recess of *Testudo geometrica* is considered to be directly homologous with the so-called paraphysis of Plagiostomes. It represents the tissues from which the more specialized true paraphysis differentiates in other animals. In the domestic fowl it is represented by both the recessus superior and the paraphysis.

In *T. geometrica* the velum transversum (*Vel. T.V.*), which bounds the supracommissural recess posteriorly, is rudimentary. It occurs where the choroid plexus of the lateral ventricles invaginate into the interventricular foramen. Its situation coincides also with the site of exit of the large chorioidal veins, which drain the chorioid plexus of the lateral ventricles. Its rudimentary appearance is to be accounted for by the fact that the supracommissural recess is proportionately smaller in *T. geometrica* than in vertebrate types such as the Plagiostomes or even in *Sphenodon punctatum*.

A third and more important recess of the roof of the third ventricle is the dorsal sac or parencephalon (*Parenceph.*), which is depicted in Fig. 5. Viewed from above (Fig. 1) this sac appears as a large rhomboidal body, longer than it is broad and surrounded by the cerebral hemispheres anteriorly and the optic lobes posteriorly. It obscures the diencephalon from view. Its centre is occupied by a large, oval depression (*S.D. Dors. Dep.*). Viewed from the lateral aspect (Fig. 2) its upper part can be seen in the interval between the hemispheres and the mesencephalic tectum, where it is evenly convex upward. Its upper surface is applied to the skull bones.

The structure of this projection is revealed in Fig. 5. It is seen to be a recess of the roof of the third ventricle, lined by ependyma and with an external covering of pia mater. The sac is most capacious superiorly, where it also lodges the choroid plexus of the third ventricle (*Pl. Ch. Vent. III*) and where the epiphysial bodies project downward and backward respectively into it. It is not definitely partitioned off into separate compartments, but its upper, anterior corner is invaginated, where a large vein passes upward from the interventricular foramen to join the superior median longitudinal vein, so that two separate anterior recesses or cornua are produced on either side. Further, the presence of the dorsal depression and the central inward projection of the epiphysial structures produces the effect of two separate halves on either side of these median structures.

The walls of this sac are very thin, consisting merely of an inner ependymal lining and an outer pial layer with no intervening tissue. They are relatively avascular, having no perforations anywhere. As this sac is an evagination of the roof of the third ventricle, its anterior wall is continuous inferiorly with the velum transversum. The anterior wall of the dorsal sac merges imperceptibly with its lateral walls. As can be seen in Fig. 5, it is inclined obliquely backward until it reaches the anterior epiphysial body (*C. Epiph. Ant.*). where it is folded sharply forward and downward. Thereafter it forms the medial walls of the two anterior cornua of the sac, connects these in front of the smaller epiphysial body and becomes continuous with the roof of the sac.

The lateral wall of the recess is attached below to the cerebral hemisphere and the diencephalon. The line of attachment to the hemisphere may in Fig. 5 be traced horizontally backward from the posterior end of the dorsal wall of the supracommissural recess. It meets the upper border of the interventricular foramen at the point where it disappears from view behind the diencephalic

eminence (*Dienceph.*). Here the lower edge of the lateral wall of the sac continues on to the latter eminence, being attached along a sharp anterior and dorsal border as far backward as the epithalamic region (*Em. Epithal.*) and the habenular commissure (*Comm. Hab.*). The inclination of the lateral wall is obliquely laterally and upward until it reaches the cerebral hemispheres, when it passes almost vertically upward until it meets the roof of the sac. Anteriorly it forms the lateral wall of the anterior cornu on each side.

The posterior wall is poorly defined from the lateral walls and roof, for all these walls together contribute towards the formation of the cylindrical posterior projection of the dorsal sac. The ependymal layer of this part of the wall of the recess is continuous in front and below, just above the habenular commissure, with the ependyma covering the neural bridge between the epithalamus and the tectum of each side. The pial layer is reflected from the external surface of this epithalamic region.

The dorsal wall or roof of the recess is more complicated. On the whole, as it is closely applied against the skull, it tends to lie horizontally, both over the depressed and elevated portions (Figs. 1 and 5). The dorsal and lateral walls consequently meet at about a right angle along almost their whole length. The sides of the dorsal depression again are more or less vertical, meeting the almost horizontal floor at about a right angle along its whole circumference. Here, along this circumference, but especially in the anterior half of the depression, the dorsal wall is invaginated into the recess to form the main body of the choroid plexus of the third ventricle (*Pl. Ch. Vent. III*). The blood vessels of this plexus also enter and leave along this line of invagination.

The epiphysial structures form conspicuous projections into this dorsal sac. As has been indicated in Fig. 5, there are two quite distinct bodies, a larger and a smaller. They are embedded respectively in the roof of the sac and in its anterior wall, lying between the ependyma internally and the pia mater externally. The smaller body (*C. Epiph. Ant.*) is oval in the longitudinal direction, circular in coronal section, thinner walled, unilocular, and gives the impression of being a cyst. No neural connexions with the brain substance could be traced on histological examination of serial sections. The larger body (*C. Epiph. Post.*) is an elongated tube which tapers at both ends, but especially anteriorly. It lies between the ependyma and the pia mater in the floor of the dorsal depression of the roof of the sac. On account of many irregular folds, which project into the lumen, but which for the sake of simplicity have not been represented in the drawing, it appears multilocular, but is not really so. The walls are relatively thicker than in the smaller of the two structures, the cells of which they are composed showing fewer signs of degeneration, and there is some evidence of secretory activity. Again no neural connexion with the forebrain could be demonstrated. It seems likely that any such connexion should be with the epithalamic region and should lie between the layers of the sac posteriorly.

The position of these epiphysial structures between the pia mater externally

and the ependyma internally is characteristic of neural tissue. Even in the absence of neural tissue in these structures, or the absence of obvious connexions with the brain it can be concluded that these are neural derivatives comparable to the pineal body in the case of the larger structure, and the parapineal body in the case of the smaller, anterior structure. In the case of the blind snake two epiphysial bodies, referred to by Von Hallerstein (1934) as the parietal eye (anteriorly) and the epiphysis (posteriorly), with no definite connexions with the brain, occur in situations rather similar to those of the epiphysial bodies in *Testudo geometrica*. They are, however, not embedded in the roof of the dorsal sac. Gisi (1907) has figured a median section of the brain of *Sphenodon punctatum*, in which she indicates the parietal eye as arising from the supracommissural diverticulum, or the paraphysis of her paper. This must be incorrect, for the parietal eye, which has connexions in the region of the habenular commissure, is actually derived from the parapineal. Kappers (1929) is in agreement with the view that the parapineal parietal eye may also be converted into a gland similar to the pineal. He considers such metamorphosis as analogous to the conversion of the nervous primordia of the hypophysis and medulla of the adrenal glands into hormonistic organs.

There are two masses of choroid tissue in the dorsal sac, but, for the sake of simplicity, these have not been drawn in Fig. 5. The main one, as has been described above, is invaginated from the walls of the dorsal depression of the roof along the anterior and the lateral edges of the larger of the epiphysial bodies. It tends to occupy most of the cavity of the recess on either side of this epiphysial body, and some of it projects downward beyond this body inferiorly and in front, so that it almost fills the interval between the two epiphysial bodies. The remaining smaller mass of choroid tissue is invaginated into the dorsal recess from its anterolateral wall just below the smaller of the two epiphysial structures.

The dorsal sac or parencephalon, which is claimed by many authors as being an essential element of the primitive reptilian brain, and which is well developed in most embryonic vertebrates, is probably best developed in the case of the Chelonia, as is suggested by the condition in *Testudo geometrica*. It certainly occurs in other reptiles, being a quite conspicuous structure in *Sphenodon punctatum*. Its posterior boundary is invariably the habenular commissure, and anteriorly it ends at the velum transversum. It thus actually belongs to the diencephalon, whereas the supracommissural recess and the paraphysis belong to the telencephalon. In the case of *S. punctatum*, and probably also in other reptiles, where a commissura aberrans pallii posterior exists, the dorsal sac is bounded anteriorly by this commissure. Kappers has designated this dorsal sac as the parencephalon. But he also refers to it as the pulvinar epiphyseos, in view of the fact that the stalk of the epiphysis runs over it, as in Plagiostomes. In the case of *Testudo geometrica* the epiphysial or pineal and the parapineal bodies are actually embedded in the walls of this sac, and in this brain the sac is thus truly a pulvinar epiphyseos.

The interventricular foramen

This is an anteroposteriorly elongated triangular slit which is wide anteriorly and tapers posteriorly, having a convex upper and concave lower margin (Figs. 4 and 5, *For. Int.-Vent.*). The latter curves round the upper surface of the forebrain bundle as it enters the medial surface of the hemisphere. Posteriorly the opening tapers to a point and eventually becomes closed by a membrane consisting of ependyma and of pia mater. It is thus bounded anteriorly by the posterior end of the septal formations; superiorly by the medial wall of the hemisphere, in which are embedded the hippocampus and the fimbria; inferiorly by the forebrain bundle anteriorly and more posteriorly by the medial wall of the hemisphere in which is embedded a cell formation, which is described by some authors as belonging to the amygdaloid complex. This foramen is, in form and size, a striking contrast to those seen in the illustrations to the articles on Lacertilia, Ophidia and Crocodilia in general, in which the tendency seems to be a great reduction in size and a rounding of the foramen.

The lateral ventricle

In Fig. 6 is represented a reconstruction of the lateral wall of the cerebral hemisphere. In discussing the lateral ventricle a description of only the outstanding features of this wall is deemed necessary, as there are no morphological peculiarities on the medial wall in this brain that are worthy of description here. In Fig. 6 the roof and the floor of the hemisphere and the bulb have been cut along the line of transition of these to the medial wall.

The lateral ventricle is relatively large when compared with the condition in the other reptiles, especially the Lacertilia, Ophidia and Crocodilia. This is due to the fact that the neostriatum (Kappers), hypopallial eminence (Elliot Smith) or dorsal ventricular ridge (Johnston) is not as massive in *T. geometrica* as in these other types.

The lateral ventricle is also continuous anteriorly with the cavity of the olfactory bulb. A slight constriction, the isthmus, indicates the transition of the one to the other (*Isthm. Vent.*).

The cavity of the relatively large olfactory bulb is less capacious than is expected, on account of the presence in it of the eminence produced by the dorsolateral bulbar invagination (*Em. Inv. D.-L. B.O.*).

The sulci of the ventricular aspect of the lateral wall of the hemisphere are of extreme importance, and the confusion which has resulted from inadequate descriptions of these has so far led to many erroneous interpretations of the internal structure of the hemispheres.

There are really only three main sulci in the lateral ventricular wall. The most central of these (*S. Endorh. Int.*) has similar topographical relationships to cell-formations internally as has the endorhinal sulcus, and at least part of it has previously been designated as, amongst other names, the internal endorhinal sulcus. Its true course, however, has not been fully described

previously. It commences anteriorly in the olfactory bulb and extends almost horizontally backward so that it immediately becomes hidden behind the eminence of the dorsolateral bulbar invagination. At the transition from bulb to hemisphere it reappears and becomes a deep fissure, which delimits the neostriatal or hypopallial or dorsal ventricular ridge inferiorly (*D.-L. Vent. Ridge*). In places it is hidden completely by this overhanging ridge. Then it becomes very shallow and by turning obliquely upward and backward it comes to lie on the surface of the ventricular ridge, down the centre of which it then runs. Its most important features are that it commences *in* the olfactory bulb and posteriorly continues on to the ventricular ridge, as described, instead of proceeding onwards below it. Johnston (1915) described it as bifurcating posteriorly in *Cistudo carolina*. The dorsal limb of

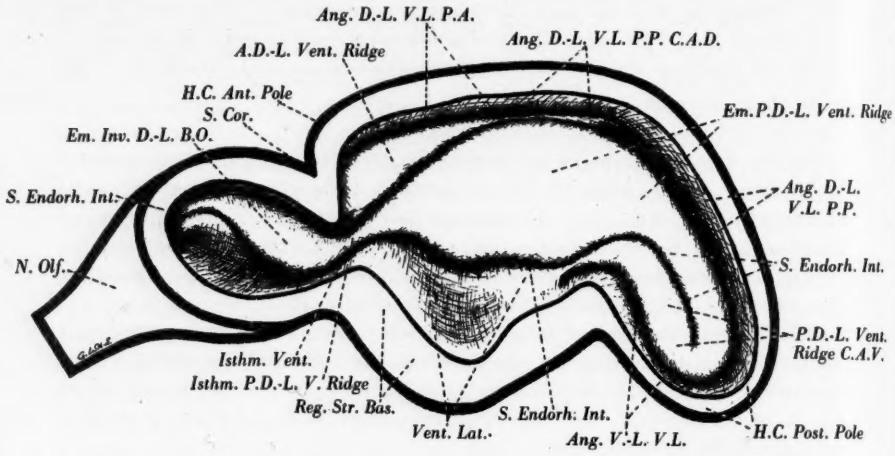

Fig. 6. A reconstruction of the lateral ventricle and lateral wall of the right hemisphere of the brain of *Testudo geometrica*. (20 × natural size.)

this bifurcation must be the true termination of the sulcus also in this animal.

The next sulcus of importance commences in the bulb as the dorsolateral angle of this part of the ventricle. At the isthmus it curves sharply upward into the anterior pole of the hemisphere and then passes upward and backward as the dorsolateral angle of the ventricle for about half the length of the hemisphere (*Ang. D.-L. V.L. P.A.*).

The third sulcus (*Ang. D.-L. V.L. P.P. C.A.D.*) commences at the isthmus and passing obliquely backward and upward it divides the ventricular ridge into an anterior small and posterior larger portion. It continues backward towards the posterior pole as the dorsolateral angle of the ventricle in the posterior half of the hemisphere (*Ang. D.-L. V.L. P.P.*). Here it curves downward and again forward as the ventrolateral angle of the ventricle

(*Ang. V.-L. V.L.*). It terminates by turning downward and medially towards the interventricular foramen and the diencephalic eminence, just below the region where the internal endorhinal sulcus passes on to the ventricular ridge. It probably corresponds to the ventral limb of the "bifurcation" of the internal endorhinal sulcus described by Johnston (1915).

The ventricular ridge thus defined by these sulci is seen in Fig. 6 to be related to the upper half only of the lateral ventricular wall. Commencing in the olfactory bulb as a slight convexity of the wall above the internal endorhinal sulcus, it expands rapidly into the eminence of the dorsolateral bulbar invagination (*Em. Inv. D.-L. B.O.*) which fills nearly the whole of the cavity of the olfactory bulb posteriorly and nearly blocks the isthmus. Then it narrows rapidly (*Em. P. D.-L. V. Ridge*) and again expands gradually into the large posterior dorsolateral ventricular ridge (*P. D.-L. Vent. Ridge*). It is bulkiest in the middle of the hemisphere and also rather pendulous. The ridge then curves downward while passing backward and becomes more cylindrical in shape and narrower. It terminates abruptly in the posterior pole of the hemispheres. The presence of the internal endorhinal sulcus passing across its middle in the longitudinal direction gives the impression that the ridge is actually continuous with the part above the sulcus, passes towards the posterior pole, then turns sharply round this sulcus downward and forward to terminate finally in a tapering end closely related to the diencephalic eminence. There is proof, which can however not be introduced here, that this is actually the state of affairs in *Testudo geometrica*.

The anterior dorsolateral ventricular ridge (*A. D.-L. Vent. Ridge*), which is much smaller, and is lodged in the anterior pole of the hemisphere, is probably the same projection as that described in *Chelone midas* by Elliot Smith (1919) as the "primordium neopallii". This homology is unacceptable. The ridge is formed by an inward proliferation of cells opposite the anterior endopyriform sulcus. There is also some degree of invagination. (This sulcus corresponds to that probably incorrectly homologized in the same paper by Elliot Smith with the fissura rhinalis.) The sulcus on the ventricular aspect separating the anterior and posterior dorsolateral ventricular ridges, though not very deep in all instances, is yet of the utmost topographical importance. It probably becomes obliterated in some other reptiles. The anterior dorsolateral ventricular ridge is bulkiest anteriorly. But its posterior tapering end may be traced for quite a distance till it disappears in the roof of the hemisphere.

SUMMARY

In this paper the external morphology of the brain, but particularly the forebrain, of the South African land tortoise, *Testudo geometrica*, is discussed. The description is based on the study of dissected specimens and cartographic reconstructions. The method of making these reconstructions is described.

The general features and the contours of the brain as a whole and the

cerebral hemispheres in particular are discussed. The large forebrain and midbrain and the rudimentary cerebellum are markedly contrasted. The olfactory bulbs are sessile.

A nervus terminalis is described. The various sulci found on the external surface are described and their comparative significance considered. The sulci which are most characteristically developed in this brain are the dorsolateral invagination of the olfactory bulb, the anterior and posterior endopyriform and the endohippocampal sulci. The dorsolateral invagination of the olfactory bulb has so far only been described in Edentata and Monotremata. The endopyriform and endohippocampal sulci have a great topographic and morphological significance with regard to internal arrangement of the forebrain cell masses.

The dorsal commissure or combined anterior pallial and hippocampal commissure is very large and lies anteriorly and superiorly to the ventral commissure (or anterior commissure). The anterior neuroporic recess is thus obliterated.

Considerable care has been taken to analyse and interpret the features of the ependymal recess of the third ventricle. A supracommissural recess, but no true paraphysis is recognizable. Consequently the velum transversum is poorly defined. The dorsal sac or parencephalon, of which a reconstruction is given, is very complicated, and has two rudimentary epiphysial structures embedded in its roof and choroidal plexuses invaginated from its lateral walls. The anterior epiphysial structure corresponds to the parapineal and the posterior represents the pineal body. In view of the relationship of these structures to the dorsal sac it is comparable to the pulvinar epiphyseos of Plagiostomes.

The interventricular foramen is very large.

The lateral and olfactory ventricles are in direct communication with one another. The ventricular ridges and the sulci of the lateral wall of the hemisphere are described and discussed. The arrangement and characters of these ventricular ridges and sulci have a profound morphological significance. These structures are very characteristically developed in the tortoise brain.

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EXPLANATION OF ABBREVIATIONS

Ang. D.-L. V.L. P.A.	Dorsolateral angle of the anterior part of the lateral ventricle.
Ang. D.-L. V.L. P.P.	Dorsolateral angle of the posterior part of the lateral ventricle.
Ang. D.-L. V.L. P.P. C.A.D.	Dorsal anterior continuation of the posterior part of the dorsolateral angle of the lateral ventricle.
Ang. D.-L. V.L. P.P. C.A.V.	Ventral anterior continuation of the posterior part of the dorsolateral angle of the lateral ventricle.
Ang. V.-L. V.L.	Ventrolateral angle of the lateral ventricle.
A. D.-L. Vent. Ridge	Anterior dorsolateral ventricular ridge.
Bulb. Olf.	Olfactory bulb.
C. Epiph. Ant.	Anterior epiphysial body (parapineal body).
C. Epiph. Post.	Posterior epiphysial body (pineal body).
Cereb.	Cerebellum.
Ch. Opt.	Optic chiasma.
Comm. Dors. H.C.	Dorsal commissure of the cerebral hemispheres.
Comm. Hab.	Habenular commissure.
Comm. Post.	Posterior commissure.
Comm. Vent. H.C.	Ventral commissure of the cerebral hemispheres.
Cornu A.S.S.D.	Left anterior cornu of the dorsal sac.
Dienceph.	Diencephalon.
Em. Epithal.	Epithalamic eminence.
Em. Hypothal.	Hypothalamic eminence.
Em. Inv. D.-L. B.O.	Eminence produced by the dorsolateral invagination of the olfactory bulb.
Em. Thal.	Thalamic eminence.
Ev. E. Cer.	Everted free lateral edge of the cerebellum.
For. Int.-Vent.	Interventricular foramen.
Fov. S.E.E.	Fovea of the external endorhinal sulcus.
H.C. Ant. Pole	Anterior pole of the cerebral hemisphere.
H.C. Post. Pole	Posterior pole of the cerebral hemisphere.
Hem. Cer.	Cerebral hemisphere.
Hypoph.	Hypophysis.
Hypothal.	Hypothalamus.
Infundib.	Infundibulum.
Inv. D.-L. B.O.	Dorsolateral invagination of olfactory bulb.
Isthm. P. D.-L. V. Ridge	Isthmus between the posterior dorsolateral ventricular ridge and the eminence of the dorsolateral invagination of the olfactory bulb.
Isthm. Vent.	Isthmus of the olfactory and lateral ventricles.
Lam. Inf.-N.-P.	Lamina infra-neuroporica.
Lam. Sup.-N.-P.	Lamina supra-neuroporica.
Med. Obl.	Medulla oblongata.
Med. Sp.	Spinal medulla.
Mesenceph.	Mesencephalon.
N. Abd.	Abducens nerve.
N. Acc.-Sp.	Spinal accessory nerve.
N. Coch.-Vest.	Cochlear and vestibular nerve.
N. Fac.	Facial nerve.
N. Gl.-Ph.	Glossopharyngeal nerve.
N. Hyp.-Gl.	Hypoglossal nerve.
N. Oc.-M.	Oculomotor nerve.
N. Olf.	Olfactory nerve.
N. Opt.	Optic nerve.
N. Term.	Terminal nerve (? vomero-nasal).
N. Trig.	Trigeminal nerve.

N. Troch.	Trochlear nerve.
N. Vag.	Vagus nerve.
Parenceph.	Parencephalon, dorsal sac or pulvinar epiphyseos.
Pl. Ch. Vent. III	Choroid plexus of the third ventricle.
Pl. Ch. Vent. IV	Choroid plexus of the fourth ventricle.
P. D.-L. Vent. Ridge	Posterior dorsolateral ventricular ridge.
Ram. Hor. S.E.E.	Horizontal ramus of the external endorhinal sulcus.
Ram. Vert. S.E.E.	Vertical ramus of the external endorhinal sulcus.
Rec. Hypothal.	Hypothalamic recess.
Rec. Inf.	Infundibular recess.
Rec. Pre-Op.	Pre-optic recess.
Rec. Sup.-Comm.	Supracommissural recess.
Reg. Amygd.	Amygdaloid region.
Reg. Diag. Bd.	Diagonal band region.
Reg. Hipp.	Hippocampal region.
Reg. Pyr.	Pyriform region.
Reg. Sep.	Septal region.
Reg. Str. Bas.	Basal striatal region.
S. Amygd. Rud.	Rudimentary amygdaloid sulcus.
S. Cor.	Coronal sulcus (S. olfactorius).
S. Endohipp.	Endohippocampal sulcus.
S. Endopal.-Olf.	Endopalaeo-olfactory sulcus.
S. Endopyr. Ant.	Anterior endopyriform sulcus.
S. Endopyr. Post.	Posterior endopyriform sulcus.
S. Endorh. Ext.	External endorhinal sulcus.
S. Endorh. Int.	Internal endorhinal sulcus.
S. Lat. Ant.	Anterior lateral sulcus.
S. Lat. Post.	Posterior lateral sulcus.
S. Lob.	Sulcus lobaris.
S. Med. Ant.	Anterior median sulcus.
S. Med. Post.	Posterior median sulcus.
S. Prim.	Sulcus primus.
S. Sept.-Cort.	Septo-cortical sulcus.
S. Sept.-Str.	Septo-striate sulcus.
S.D. Ant. Wall.	Anterior wall of the dorsal sac.
S.D. Dors. Dep.	Dorsal depression of the roof of the dorsal sac.
S.D. Lat. Wall	Lateral wall of the dorsal sac.
S.D. Post. Pole	Posterior pole of the dorsal sac.
S.D. Roof	Roof of the dorsal sac.
Tect. Mes.	Mesencephalic tectum.
Tr. Opt.	Optic tract.
Tub. Olf.	Olfactory tubercle (palaeo-olfactorium), overlying the basal striatal cell masses.
Vel. T.V.	Velum transversum.
Vent. Lat.	Lateral ventricle.
Vent. III	Third ventricle.
Vent. IV	Fourth ventricle.

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AN ANATOMICAL STUDY BY INJECTION TECHNIQUE OF THE EJACULATORY DUCTS AND THEIR RELATIONS

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This study was undertaken because of the lack of uniformity in the descriptions given in the literature. In view of the importance of the ejaculatory ducts as the direct communication of the testicular system with the urethra, it is surprising that more detailed investigation has not previously been undertaken. The most recent work was carried out in 1932 by McCarthy & Ritter (1932), who followed their investigation with the introduction of a new method of catheterizing the ducts. The present work involved the examination of more than one hundred specimens. These were obtained fresh from autopsy in most cases and were injected with solution as soon as possible. The subjects were adults of varying ages; although exact records of age could not be kept, there did not appear to be any marked variations with age. The work was undertaken to determine the exact course of the ducts through the verumontanum (urethral crest). The initial work consisted of careful dissection under the dissecting microscope of specimens fixed in formalin and it was found that the ducts appeared to open into the utricle in 4 out of 10 cases examined. This possibility is described by every writer previous to McCarthy and his associates, although they vary as to the frequency with which the condition occurs. Ancel & Watrin (1920) state that either one or both ducts opened into the utricle in 13 cases out of 40 examined. Rolnick (1926) states that the mouths of the ducts are found more frequently on the lips of the utricle than on the verumontanum as usually described. He states also that the ducts often open on the inner lip of the utricle and in some cases they may be found on the floor of the utricle. Ainsworth-Davis (1936) states that it is not always possible to see the openings of the ejaculatory ducts, but an attempt should be made by looking into the sinus pocularis (utricle). McCarthy *et al.* (1927) state that in none of the specimens examined by them were the ducts seen to open into the cavity of the utricle, on the margins of the utricle or within 1 mm. of this margin.

Simple dissection even under the dissecting microscope was felt to be unsatisfactory. Celloidin injection and maceration in hydrochloric acid (one method used by Hyams *et al.* (1932) gave poor results owing to the bulk of the

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vesicles and the urethra, and the extreme fineness of the ducts at their termination. As the condition of the ducts at their termination was the real object of our study this method was abandoned. Injection with barium gelatin, a method used in the study of 37 specimens by Ivanizky (1928), was tried and specimens X-rayed, but this method did not give sufficient detail to make it worth while continuing. Finally the ducts were injected with gelatin and either dissected or cleared by a modified Spalteholtz method.

METHOD

The bladder together with the vasa, vesicles and prostate were removed *en bloc* in the autopsy room. The redundant tissue was removed and the vasa were then injected with warm 20 % gelatin solution (coloured with indian ink) until the solution had distended the vesicles and had flowed for a short time from the ejaculatory duct orifices. The specimen was cooled and allowed to stand in 10 % formalin for 8 days. At this stage it was either dissected under the microscope or was cleared by a modified Spalteholtz method used by Dr Saunders in his department of Anatomy at the University of California. This method gave excellent cleared specimens for study. The method of injection varied in some cases used for special study. Only those specimens which were injected and in which the course of the ducts could be described with absolute certainty (numbering in all 100 specimens) were accepted for study. All measurements given in this paper are those obtained by micrometer in cleared specimens unless otherwise stated, and in considering fresh specimens due allowance must be made for contraction during dehydration. The ejaculatory ducts are described as beginning at the junction of the vas and seminal vesicle and terminating at the verumontanum (urethral crest). The term proximal is used in the sense of being farther from the external sphincter and the term distal as being nearer the external sphincter.

Anomalies. The only anomaly found was a complete absence of the right vas, vesicle and duct in specimen No. 17 (Fig. 1). The right kidney and ureter were also absent, as was to be expected in a failure of development of the mesonephric duct. The testicles were present. This specimen also had the largest utricle seen with a patent orifice (1·9 cm. in length, 0·6 cm. in width). Schwarzwald (1928) collected 54 cases in which there was absence of the vas, vesicle and ejaculatory duct and stated that in nearly all there was accompanying congenital anomaly of the kidneys. In none of our cases was there absence of the ejaculatory duct or absence of the vesicle except as described above. Ancel (1919–20), after examination of 22 cadavers, reported 4 cases of absence of the ejaculatory duct with its place taken by separate ducts for seminal vesicle and vas. The method used was the passing of silk thread along the various ducts. We found no indication of this anomaly and Ancel's observations seem open to question. We did not find any cases of fusion of the ducts or of abnormal openings of the ducts in the posterior urethra described by Schwarzwald and also by Picard.

Length of the ejaculatory ducts. The measurements (in cm.) obtained in 66 specimens are given in the table below.

	Greatest	Least	Average	Standard deviation
Length of right ejaculatory duct	2·1	0·9	1·46	$\sigma = \pm 0{\cdot}29$
Length of left ejaculatory duct	2·1	1·0	1·47	$\sigma = \pm 0{\cdot}28$

The ducts were usually of the same length but the right duct was longer than the left in 8 cases, and the left longer than the right in 7 cases. The difference in length was seldom more than 1 mm., but in one specimen it was as much as 3 mm.

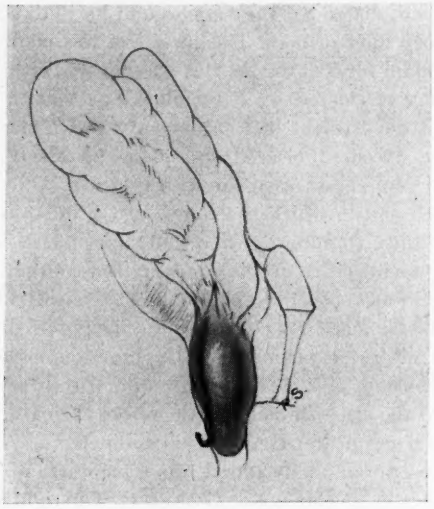

Fig. 1. Specimen No. 17. Posterior view. Dissection shows complete absence of the vas, seminal vesicle and ejaculatory duct on the right side.

Diameter of the ducts. Proximally the ducts were found to be a continuation of the short wide duct of the seminal vesicle, as pointed out by A. E. Bothe (1932). At this point they were round and of widest diameter. In the mid-portion the ducts were still round but were generally considerably smaller in diameter. In the last 7 to 5 mm. from the orifice the ducts were strap-like—thin in antero-posterior view and wide in lateral view. In the last 1 to 2 mm. the ducts often widened again, but this was sometimes more apparent than real, being due to twisting and alteration in direction of the "strap". The measurements obtained in 79 specimens are shown in the accompanying table.

Diameter (in mm.) of the ducts as seen in anterior view

		Greatest	Smallest	Average	Standard deviation
Proximal portion:	Right	3·5	0·5	1·31	$\sigma = \pm 0{\cdot}54$
	Left	3·5	0·3	1·41	$\sigma = \pm 0{\cdot}68$
Middle portion:	Right	2·0	0·2	0·93	$\sigma = \pm 0{\cdot}39$
	Left	2·0	0·2	0·95	$\sigma = \pm 0{\cdot}40$
Terminal portion:	Right	1·0	0·1	0·45	$\sigma = \pm 0{\cdot}17$
	Left	1·1	0·1	0·50	$\sigma = \pm 0{\cdot}20$

Differences in the two ducts. Apart from slight variations in length and width, the similarity of the two ducts in each specimen was remarkably constant.

Diverticula. These were seen in only 7 cases; five times on the right side, once on the left, and once bilateral. These diverticula were always situated in the proximal part of the ejaculatory duct within a few millimetres of the seminal vesicle and were generally on the medial and posterior aspect. These had the appearance of rudimentary vesicles with a fine duct leading into the ejaculatory duct (Fig. 2) and were not merely simple pouches of the lining membrane of the ejaculatory duct.

Sinus ejaculatorius. Felix (1901) described a dilatation of the proximal part of the duct, which he called the sinus ejaculatorius. Jacques Despouys (1923) again described "une sorte de renflement ovalaire" which he called the "sinus éjaculateur". In our specimens, in only 11 cases did we find a slight constriction about 2 mm. distal to the origin of the duct, which would enable the proximal portion to be described as a sinus. We did not see anything resembling the diagrammatic drawing of Despouys. The condition was present on the right side alone, twice; on the left side alone, twice; and bilateral in 7 cases.

We found that in six of our specimens the postero-medial wall had an irregular edge, as shown in Fig. 3. This gave it a distinctly "feathered" appearance. We could find no evidence of the five recesses on the dorsal and medial walls described by Felix.

Course of the ducts. The average distance separating the ducts at their origins was about 2 mm. They came into closest apposition within a few millimetres of their termination and at this point they began to curve laterally in most cases. In many this consisted of a gentle uniform curve, as shown in Fig. 4, but in others the curve was so pronounced, as shown in Fig. 5, that the termination could be fitly described as "hooked". McCarthy and his associates describing the course of the ducts from their orifice at the urethra towards the seminal vesicles says: "they diverge for the first millimetre and a half and then converge for the next millimetre or two until there is a thin septum of fibrous and elastic tissue separating them." We did not see anything which would correspond to this description in any of our specimens. We found that the ducts proceed straight to their termination, as described in Gray's *Anatomy* (1936) without any medial or lateral curvature. There is a forward curve as the duct rises to open on the surface of the verumontanum, in 19 cases of the

Fig. 2.

Fig. 3.

Fig. 2. Diverticula of the right ejaculatory duct.
Fig. 3. Specimen No. 99. Note the "feathered" appearance of the medial wall of the duct. The relationship of the terminal portion of the ducts to the utricle in this case is well shown.

Fig. 4.

Fig. 5.

Fig. 4. Gentle outward curvature of the terminal portion of the ducts.
Fig. 5. Marked curvature of the terminal portion of the ducts.

94 specimens available for this study, i.e. 20·2 % (Fig. 6). In the remainder, the ducts, which have been drawing closer together in their course through the prostate, diverge in the last few millimetres. In 53 % they have a gentle lateral curve (see Fig. 4); in 23 % the curve is sharper and of greater degree (Fig. 7); and in 24 %, the curve is so marked that it resembles a hook (see Fig. 5). In these latter cases the duct rises to the surface of the verumontanum separated from the duct of the opposite side by the utricle, and as it approaches the mucosa it turns laterally beneath it and then follows the curve of the lateral face of the verumontanum to its orifice on the side of the verumontanum.

Fig. 6. The straight type of duct. The long utricle occupies the space between the ducts.

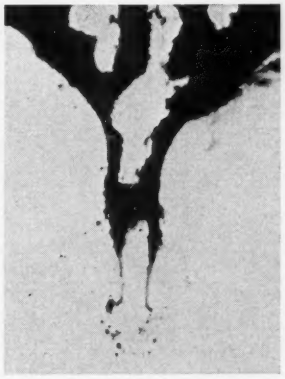

Fig. 7. Ducts with a medium degree of curvature at their termination.

In some cases the terminal portion was not only directed towards the floor of the prostatic sinus, but also proximally, i.e. the hook-like termination of the duct lay in a plane at an angle of about 60 degrees to that of the floor of the urethra.

Do the ejaculatory ducts ever open into the utricle? Ancel & Watrin (1920) say this occurs in 33 % of cases. McCarthy *et al.* did not find this in any of their cases. In 4 cases in our series one duct opened into the utricle and in one case both ducts opened into the utricle (Fig. 8). In no case did we find the duct terminating in the utricle as so frequently described by the older authorities.

In each case where an opening existed between the ducts and the utricle we were able to show that this was either due to a developmental or pathological breakdown of the thin wall between the duct lumen and the utricular cavity. In each case we were able to trace the continuation of the duct with its customary lateral curve to a normal ejaculatory duct opening on the surface of the verumontanum.

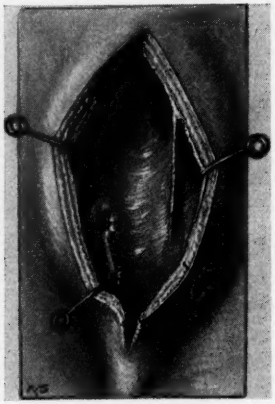

Fig. 8. Specimen No. 39, after incision of the anterior wall of the utricle. The terminations of the ducts were in the usual situation on the surface of the verumontanum and were patent, although that on the right side was small and is obscured in the drawing by eversion of the cut margin.

The seminal vesicles. Sixty-nine cleared specimens are available for study. The measurements (in cm.) obtained are given in the accompanying table:

		Greatest	Least	Average	Standard deviation
Right vesicle:	Length	5·6	1·5	3·2	$\sigma = \pm 0{\cdot}87$
	Width	3·0	0·5	1·3	$\sigma = \pm 0{\cdot}46$
Left vesicle:	Length	6·0	1·3	3·1	$\sigma = \pm 0{\cdot}90$
	Width	3·2	0·4	1·2	$\sigma = \pm 0{\cdot}45$

Georges Luys (1930) gives the length of the vesicles as from 4 to 11 cm. and the breadth as from 1·5 to 3·0 cm., but he does not state whether these measurements were obtained in fresh filled specimens or not. We have no measurements for fresh filled specimens, but we find a reduction of 18 % in our measurements for cleared specimens as compared with our measurements for fixed. Schultz (1919) states that there is 2·54 % shrinkage when a specimen is fixed in 10 % formalin for 36 weeks, but reduction in measurements given above is not wholly due to further shrinkage in dehydration (elsewhere, p. 567, we show a reduction in measurements due to dehydration of 13·5 %) but to the fact that cleared measurements were made of the cavity of the vesicle and not of its external surface, thus length is taken as from the junction of the vas and

vesicle to the tip of the cavity of the vesicle and width as the greatest distance from one side of the cavity to the other. Inman & Saunders (1937), discussing shrinkage in specimens dehydrated with gradually increasing concentrations of alcohol, state that there is "distinctly more than 2 %" (the amount which they had just recorded for another method), but do not say just how much.

A great deal of discussion has centred on the observation of Belfield that whether the injection is from the vas above or from the duct below, the vesicle always fills first and then the flow extends to the ejaculatory duct or to the vas respectively. Belfield (1913) explained this by describing a sphincter at the exit of the duct which prevented flow along the duct when the vas was injected. The irregularity and cellular nature of the lining membrane of the ampulla of the vas similarly offered obstruction and caused filling of the vesicle when the ejaculatory duct was injected. To explain the filling of the vesicle when the vas is injected, Hochstädt (1931–2) postulates a sphincter muscle which lies a millimetre or two from the junction of the duct of the seminal vesicle and the vas. In 11 of our specimens there was a slight constriction at this point, as described above, but this did not suggest a definite sphincter, and one could not expect a sphincter to play a part in cadaver material. We found that the ampulla invariably joins the duct of the seminal vesicle on the posteromedial aspect, as stated by McCarthy and his associates. We found in 66 cleared specimens in which the junction was plainly visible that the vas opened into the vesicle at an acute angle (about 30 degrees) in 47 %; at about 45 degrees in 13 %; at about 60 degrees in 13 %; at 90 degrees in 25 % and in one case was turned back on itself to open into the vesicle at an obtuse angle. In 20 % of these cases, the angle of junction was different on two sides. That the junction may vary on two sides is well seen in the vesiculogram shown by Voelker & Boeminghaus (1928).

The ampulla is comparatively wide—average width of lumen from 2 to 3 mm.—and its lining membrane is heaped into ridges, making its lumen very irregular, but, no matter how wide or how irregular the lumen of the ampulla, the lumen of the last millimetre or two is always smooth and seldom more than 1 mm. in diameter. Belfield states that anastomoses between the dilated extremity of the vas (i.e. the ampulla) and the vesicle are not rare. No evidence of any such condition was seen in our specimens.

It has been pointed out—originally by Ivanizky—that the duct of the seminal vesicle and the ampulla join at varying angles so that the ejaculatory duct may be either a continuation of the seminal vesicle, or of the vas, or may be midway between these positions. These observations have been made on external examination of the ducts and are not borne out by our observations. In all cases we found that the duct of the seminal vesicle continued into the ejaculatory duct as a gradually narrowing funnel and that the vas joined this gradually narrowing funnel as described above. It is obvious that the filling of the vesicle requires only a mechanical explanation and not a physiological one. When fluid is injected into the vas it flows into the lower end of the

vesicle, which has a wide bore, and fills the vesicle until the tension is sufficient to overcome the mechanical resistance of the ejaculatory duct with its gradually diminishing bore. In one of our specimens the vesicle filled satisfactorily although the ejaculatory duct had been cut across at its mid-point. When fluid is injected into the ejaculatory duct it readily flows into the vesicle and will only extend out along the ampulla and vas when tension in the vesicle is sufficiently high. The seminal vesicle consists of a coiled tube about 15 cm. in length with numerous diverticula, but what is not generally recognized is that

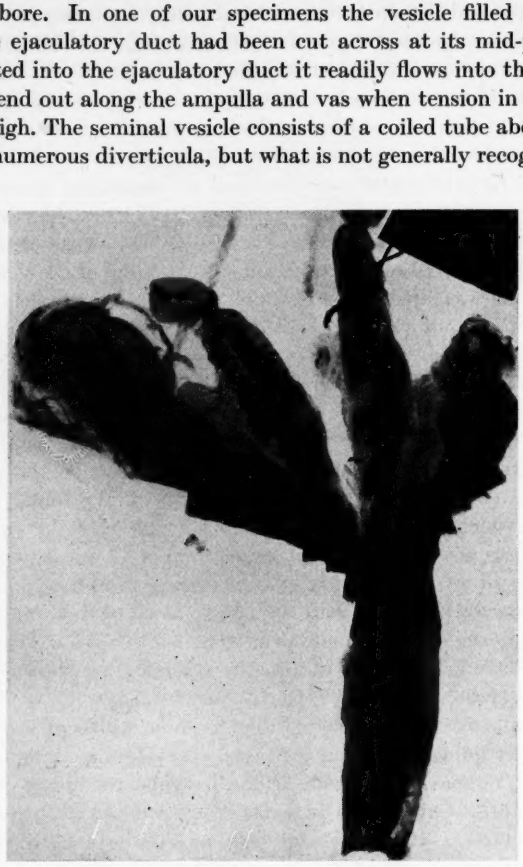

Fig. 9. Specimen No. 88. Note how the injection material only extends a short way into the vesicles, because they are already filled with secretion.

this coiled tube is itself a blind diverticulum and that there is no inlet and outlet as, for example, in the coiled tube of the epididymis. It can thus be seen that if fluid is injected into a vesicle already almost full of secretion, it will only flow along the vesicular tube until the tension is sufficient to cause fluid to flow from the ejaculatory duct orifice. Thus in 41 % of our specimens we found the vesicles on one or both sides only partially filled with gelatin, while the rest of the vesicle was filled with secretion as could be seen beautifully in our cleared specimens (Fig. 9). In 16 % this was so extreme that

the vesicle was not filled except for a few millimetres of its duct and yet there was no evidence of obstruction.

Anomalies of the vesicles. Few were observed. There was marked variation in size irrespective of the age. There was complete absence of one vesicle (Fig. 1). There was doubling of the left vesicle in one case—Specimen 61 (Fig. 10). The upper vesicle consisted of a straight tube and the lower vesicle consisted of the usual coiled tube. There was a distinct plane of cleavage in the fascia between the two. The vas and upper vesicle joined and the duct thus formed joined the duct of the lower vesicle. A similar diverticulum arising

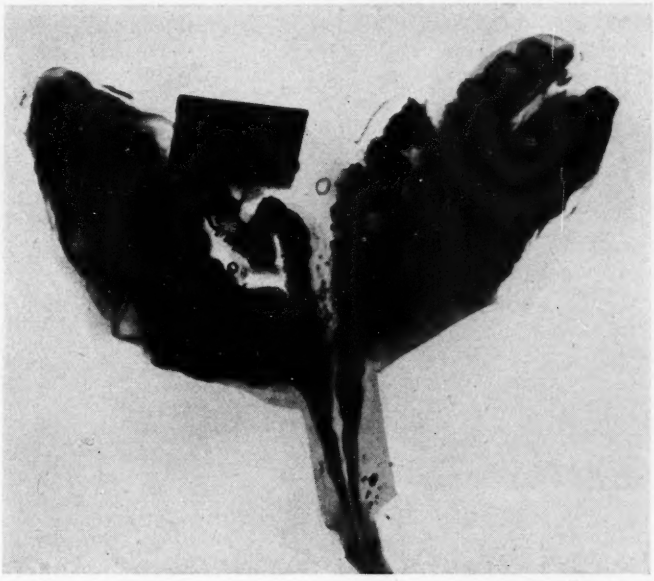

Fig. 10. Specimen No. 61. Complete duplication of the left seminal vesicle.

from the ampulla of the vas existed on the right side in specimen No. 60 (Fig. 11) but only extended along the upper border of the right vesicle for a third of its length and ended blindly. Georges Luys (1930) states that most examples of this anomaly recorded are probably bifid terminations of the vesicle, but accepts one case recorded by Heckardt as authentic.

The utricle. Measurements were available in 23 cases. In 16 cases the utricle was injected before clearing and in 6 cases the utricle was split open for inspection. The measurements (in mm.) are shown in the accompanying table:

	Greatest	Least	Average	Standard deviation
Length of utricle	19	4	9·8	$\sigma = \pm 3{\cdot}8$
Breadth of utricle	6	1	2·5	$\sigma = \pm 1{\cdot}9$

In 5 cases the ejaculatory ducts opened into the utricle as described above.

Our main interest in the utricle was to determine its relationship to the ejaculatory ducts and we found in 6 fixed specimens, in which the utricle was opened by incising its anterior wall, that the ducts could be seen either on the lateral wall or the posterolateral wall except in the most proximal portion where the ducts gradually move posteriorly to lie deep to the utricle. In these specimens also the ducts were only separated from the cavity of the utricle by a very thin wall, and there was a furrow in the posterior wall or floor of the utricle separating the two ducts. The relationship of ducts and utricle was also studied in 16 specimens in which the ducts were injected via the vasa and the

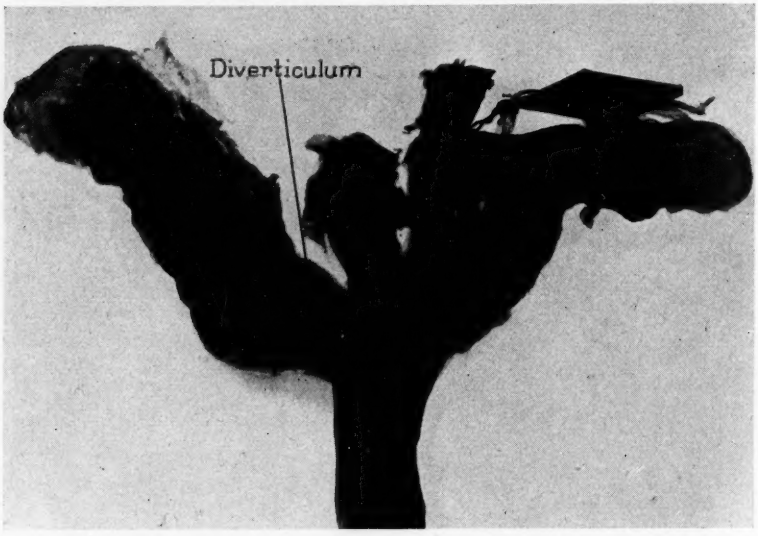

Fig. 11. Specimen No. 60. Rudimentary double vesicle on the right side.

utricle was injected with white contrast gelatin. In 14 of these the distal few millimetres of the utricle lay between the terminations of the ducts and in 2 it lay in the midline slightly anterior to the ducts. This is shown well in Fig. 12, and in the photomicrograph in Fig. 13. Beyond the first 5 mm. the utricle, as stated above, tends to lie anterior to the ducts, although in 56 % of the specimens in which this problem was investigated the utricle lay between the ducts throughout most of its length.

The verumontanum. This was measured in 38 specimens. In 28 cleared specimens the measurements (in mm.) were as follows:

	Greatest	Least	Average	Standard deviation
Length of verumontanum	12	7	9·0	$\sigma = \pm 1{\cdot}7$
Breadth of verumontanum	6	3	4·0	$\sigma = \pm 1{\cdot}8$

In 10 fixed specimens as follows:

	Greatest	Least	Average	Standard deviation
Length of verumontanum	18	7	10·4	$\sigma = \pm 3{\cdot}0$
Breadth of verumontanum	6·5	4	4·58	$\sigma = \pm 0{\cdot}9$

In specimen No. 28, which was measured both in fixed and cleared states:

Fixed ... ... Length 9 mm. Breadth 4·6 mm.
Cleared ... ... Length 8 mm. Breadth 4·0 mm.

These figures show on average about 13·5 % loss in length with clearing and this corresponds to measurements in the single specimen No. 28. McCarthy gives the average length of the verumontanum as 9 mm. and the width as 3 mm. Quain (1914) gives the length as about 15 mm., but difference of opinion may arise due to the fact that the verumontanum tapers off both proximally and distally.

Fig. 12.

Fig. 13.

Fig. 12. Specimen No. 94. Posterior view. Note how the ducts proceed along the posterolateral wall and then curve forwards lateral to the utricle to terminate with a distinct outward curve at the point indicated by arrows.

Fig. 13. Transverse section which shows the close relationship of the ducts to the lateral walls of the utricle.

We were, however, most interested in the appearance of the opening of the utricle and the general appearance of the verumontanum and have classified two main types from a study of 60 specimens. In 8 of our specimens we could not see any opening to the utricle even with the dissecting microscope.

Type 1. The verumontanum forms a smooth elongated mound in the floor of the posterior urethra and the orifice of the utricle is seen as a circular or horseshoe-shaped opening in the midline on the distal incline, while the ejaculatory duct openings are generally a millimetre or so proximal to it, as shown in Fig. 14. If the opening is small, it may be difficult to distinguish, but if a probe is passed proximally over the surface of the verumontanum in the

midline it catches readily in the anterior lip. In this type, the anterior covering or roof of the verumontanum is thin and lifts readily on a probe. If the opening is larger, the floor of the utricle which is rough can be easily seen and makes the edges of the opening stand out by contrast. If the opening is quite large, the terminal portions of the ejaculatory ducts are exposed as they lie along the posterolateral wall—as they project they resemble guns projecting from a gun-turret, and Georges Luys has aptly called them "Canons de fusil". This condition was present in 3 of our specimens (Fig. 15). Luys believes that cauterization of the verumontanum is the explanation but one feels that cauterization which would be sufficient to destroy the surface of the verumontanum would not be likely to leave the very delicate walls of the ducts

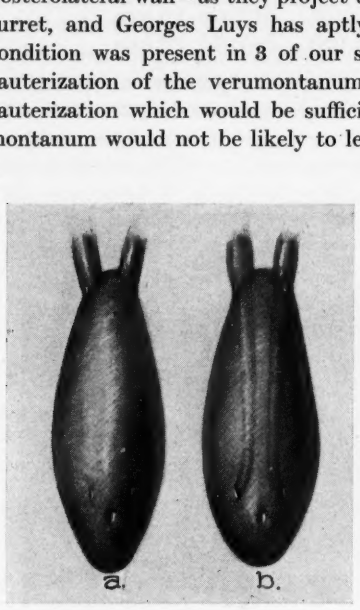

Fig. 14.

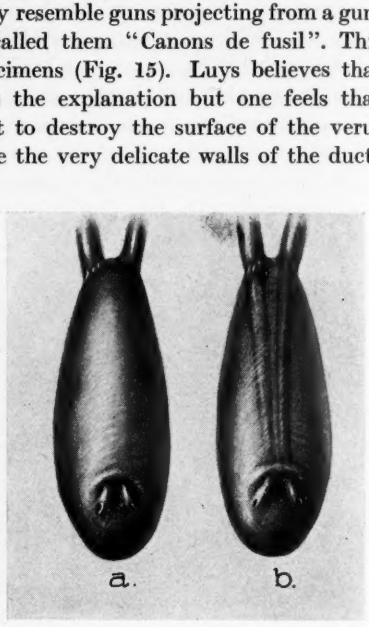

Fig. 15.

Fig. 14. *a* and *b* are two examples of verumontanum described in the text as type 1.
Fig. 15. Verumontanum in which the orifice of the utricle is large. Its anterior margin is retracted, exposing the ejaculatory ducts lying in floor.

intact. An excessive amount of retraction of the anterior lip of the orifice of the utricle in this type I verumontanum would be a sufficient explanation. In this type I verumontanum the ejaculatory ducts extend from the surface of the verumontanum backwards and proximally either in almost a straight line or with a very gentle curve medially, as shown in Fig. 4. This type was seen in 60 % of our specimens.

Type 2. The verumontanum is elevated as before but its summit is occupied by an elongated slit—the orifice of the utricle (Fig. 16)—and the sides of this slit are in some cases elevated and rolled outwards, reminding one of the appearance of the cervix uteri, as shown in Fig. 17. Where this condition was present the ducts were found to open just distal to the transverse axis of the

utricular orifice and it was in cases of this type that marked curvature or "hooking" was found in the terminal portion of the ducts.

This type was found in 40 % of our cases.

Considerable interest has been displayed by anatomists as to the proportion of cases in which openings of the ducts were proximal or distal to the orifice of the utricle. Young (1926) stated that the ducts usually empty below the utricle, but may lie alongside it or above it. We found the openings proximal to (above) the orifice of the utricle in 40 %; distal (below) in 14 %; and in line with the transverse axis of the utricular orifice in 46 % of 70 cases examined. If the openings of the ducts are proximal to the orifice of the utricle (this nearly always occurs in a type 1 verumontanum) the terminal portions of the ducts are generally straight or only slightly curved.

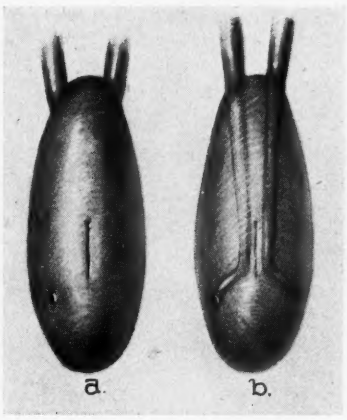

Fig. 16.

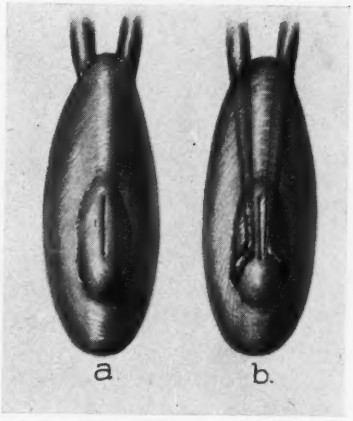

Fig. 17.

Fig. 16. Verumontanum described in the text as type 2.
Fig. 17. Verumontanum in which the orifice of the utricle appears as a longitudinal slit with rolled edges, elevating it from the smooth contour of the verumontanum.

Trigonal muscle. In dissection of fixed specimens it was found that the fibromuscular tissue surrounding the vesicles was continued down along the ducts, and this tissue contained many blood sinuses as described by Testut. Testut (1931) and later McCarthy described this as surrounding the ducts, but we found it gathered into a stout strand which lay along the dorsum of the ducts and between them proximally. Distally this strand became narrower and ended in the fibromuscular tissue at the distal end of the verumontanum. In specimens Nos. 62 and 7 a sheet of tendinous fibres was found to sweep over the terminal portions of the ducts in fan-like manner, as shown in Fig. 18. This sheet appeared to be continuous with the tendon of the trigonal muscle, which ends at the proximal end of the verumontanum, and became fixed distally in

the fibrous tissue of the urethral floor distal to the verumontanum. This suggested that contraction of the trigonal muscle might have some constrictor action on the ejaculatory ducts at their termination. It was found that the trigonal muscle could be separated by sharp dissection from its attachment to the trigone of the bladder, and that blunt dissection thereafter readily freed it from the outer aspect of the bladder neck and floor of the posterior urethra as far as the verumontanum. From the bladder neck the tendinous fibres spread out fan-wise and traction without further dissection was found to produce straightening of the urethra, some elongation of the verumontanum and approximation of the posterior part of the lateral walls of the urethra towards the verumontanum, so tending to narrow or shut off the prostatic sinuses. Wesson (1920) states that in the living subject the trigonal muscle can

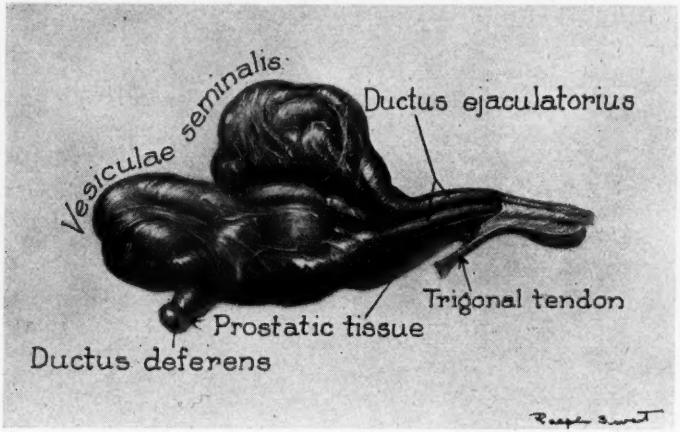

Fig. 18. Dissection of specimen No. 62. This shows a well-defined sheet of fibres extending from the trigonal tendon and sweeping around the termination of the ejaculatory ducts.

be seen to exert a direct upward pull on the verumontanum. It was found also that the central part of the tendon of the trigonal muscle formed a stout band which was inserted into the proximal part of the verumontanum and which we traced subsequently around the terminations of the ejaculatory ducts and utricle. Experiments with fresh specimens showed that if fluid was flowing in a steady stream from both ejaculatory orifices under 18 in. pressure the flow could be stopped by traction on the tendon of the trigonal muscle.

In 5 cases fresh specimens were fixed on a board and the trigonal muscle was dissected free. The vasa were freed and needles inserted. Warm gelatin was allowed to flow through these from an elevated container. This soon appeared at the ejaculatory duct orifices and discharged in a steady stream. Traction on the trigonal muscle stopped the flow in all cases and the muscle was pinned down in this position. The specimen was chilled, fixed and cleared. Examina-

tion of these specimens shows that in the last 4 or 5 mm. the ducts which normally tend to be flattened from side to side in this portion were so constricted as to have the gelatin expressed from the lumen, while just behind this point the ducts were well filled (Fig. 19).

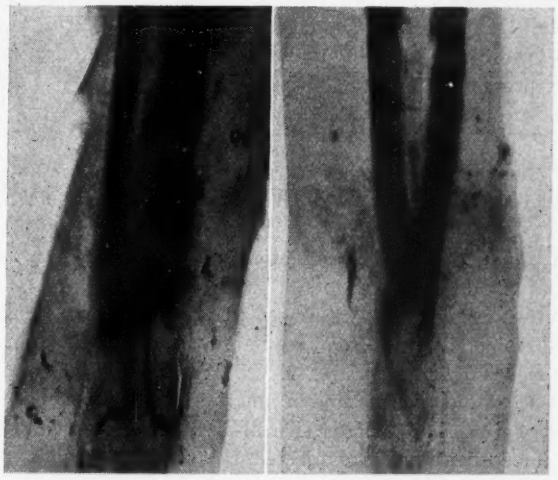

Fig. 19. Specimens Nos. 101 and 102. These show how the terminal portions of the ducts are constricted as result of traction on the trigonal muscle. Compare with Fig. 9.

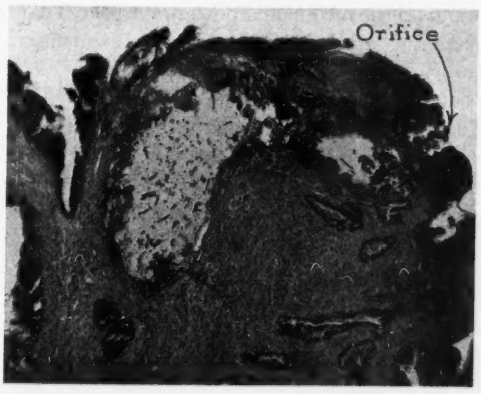

Fig. 20. Photomicrographs of specimen No. 18. Transverse section through the curved termination of the ducts. Arrow points to the orifice of the duct. This section—one of a series—shows that the duct not only curves laterally and posteriorly, but also proximally, i.e. the orifice is proximal or nearer the bladder than the middle portion of the curve.

Fig. 20 shows a transverse section through the termination of one duct (specimen No. 18) which showed "hooking". This shows the overhanging fold

of mucosa which was described by Lowsley (1912) as a flap-valve to prevent regurgitation of fluids along the duct. Our observations show that no such valve exists except in sections through these "hooked" specimens (i.e. in about 20 % of cases). Lowsley also described how the terminal portion of the ducts run for a short distance just beneath the mucosa of the verumontanum and considered that this probably also had some effect in preventing regurgitation. This type of termination was only found in 7 of our cases and in most of these was not very pronounced.

CONCLUSIONS

(1) That the ejaculatory ducts average 1·47 cm. in length and taper from an average of 1·35 mm. at the proximal end to an average of 0·475 mm. at the orifice.

(2) That the duct lumen is essentially a continuation of the tapering duct of the seminal vesicle.

(3) That the ampulla of the vas always joins the seminal vesicular duct with a constricted lumen and most frequently at an acute angle, but in about 25 % of cases at a right angle.

(4) That because of this method of junction and because of the tapering of the ejaculatory duct, the seminal vesicle always fills before fluid flows from the ejaculatory duct when the vas is injected, and also the seminal vesicle always fills before fluid travels along the vas in retrograde injections.

(5) That difference in ducts in any one case is uncommon.

(6) That diverticula are rare. They occur only in the proximal part of the ejaculatory duct and on the medial and posterior aspect. That these diverticula are glandular in structure and join the duct with an extremely fine lumen. They are not outpouchings of the lining of the duct.

(7) That in 4 of our specimens one duct opened into the utricle and in one specimen both ducts so opened, but that these openings were due to a break-down in the septum separating the duct from the lumen of the utricle and not to the ejaculatory duct terminating in the utricle as so frequently described.

(8) That in only 11 % of cases was the dilatation of the proximal end of the ducts sufficient to warrant this portion being described as a sinus.

(9) That if the vesicles are already full of secretion, the amount of injection medium that enters the vesicle is small.

(10) That the utricle in many cases lies between the ejaculatory ducts through part of its length.

(11) That the verumontanum can be classed into two main types, (*a*) with a round utricular opening on its distal incline, or (*b*) with an elongated slit-like opening on its summit. That in the first type the ducts can be expected to proceed with only a slight medial curve, or, even without a curve, proximally and posteriorly towards the vesicle. That in the second type the ejaculatory ducts can be expected to proceed medially from the orifice with a curve convex to the observer, until they come into apposition with the wall of the utricle,

when they proceed proximally along the wall and somewhat posteriorly towards the vesicle.

(12) That whatever action the trigonal muscle may have in opening the bladder neck, it undoubtedly has power when contracted to reduce the width of the prostatic sinus and more particularly, by means of a tendinous extension which sweeps around each ejaculatory duct, to close these ducts.

SUMMARY

1. The anatomy of the ejaculatory ducts and seminal vesicles was investigated by injection technique followed by clearing with a modified Spalteholtz method.

2. The reason for the filling of the seminal vesicles on injection was found to be due to the relative diameters of the lumina of the vesicles and ducts.

3. The vesicles, if already full of secretion, will not fill further with injection medium.

4. The terminal portions of the ducts often show a sharp lateral and posterior curve before opening on the verumontanum.

5. The appearance of the verumontanum is a guide as to whether the ducts are likely to proceed direct proximally from the orifice or whether they are likely to curve sharply medially before doing so.

6. The trigonal muscle ends in a tendon which spreads fan-like over the last few millimetres of the lateral wall of the ejaculatory duct on each side, and the contraction of this muscle, during urination, compresses the terminations of the ducts and prevents any possibility of back flow.

Our thanks are due to Dr J. B. de C. M. Saunders, Chairman of the Division of Anatomy, University of California Medical School. Dr Saunders placed the full resources of his department at our disposal, including the services of Research Assistant, Mr R. Skarda.

Thanks are also due to Dr Jesse Carr and his associates of the Department of Pathology, University of California Medical School, for their help in securing the material for this study.

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NOTE ON THE INTERNAL ARCHITECTURE OF THE MANDIBLE

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Gullberg & Burkitt (1924) stated that although the Piltdown jaw in its external form resembled the jaw of chimpanzee, yet its internal architecture was that of a powerfully developed human jaw. This statement, if true, would throw doubt upon the accepted functional interpretation of the internal architecture of bone. According to the usual interpretation of bone structure, the internal architecture of the jaw should be in conformity with its external form, and there would be no reason why the internal form should add anything to the external form as a means of determining zoological position.

There is general agreement that the opening and closing movements of the mandible take place around a transverse axis (not absolutely fixed, but travelling a little backwards and forwards) which corresponds approximately with the line joining the two inferior alveolar foramina. The ascending and the horizontal rami move on the arc of a circle, the former being drawn forwards by the lateral pterygoid, and backwards by the posterior fibres of the temporal muscle. The closing muscles, though several in number, are, from the functional point of view, one group, and exert their force at the junction of the horizontal with the vertical ramus of the mandible in front of the transverse axis. The contact of the teeth of the horizontal ramus with those of the upper jaw prevents the condyle being driven against the base of the skull. The closing force is naturally greatest in the region of the last molar tooth, and gradually diminishes as one passes forwards.

Thus we can regard the jaw, from the condyle to the symphysis, as a beam whose approximation to a horizontal direction is more readily appreciated if we omit the muscular processes, the coronoid and the angular. This beam is forced upwards by the closing muscle mass. Behind it may be regarded as loaded from above by the downward thrust of the base of the skull and in front by the teeth of the upper jaw. The elementary statics of such an arrangement have been described and illustrated by Murray (1936). The trajectorial lines of compression would follow the lower border, and those of tension the upper border of the beam. These would cross orthogonally near the extremities (the condyle and the symphysis) and between the two would lie the neutral region.

This simple picture is disturbed by the teeth. Each tooth is surrounded by a root sheath of compact bone from which short trabeculae extend in all directions. The teeth and alveolar margin change the upper compact trajectorium

(T. dentale) into a close mesh of horizontal lamellae. On the front of the ascending ramus behind the teeth the compactness of this trajectorium is visible, but it is more loosely arranged as it crosses the base of the coronoid process towards the condyle.

Along the lower border the trajectorium basale is made of compact bone, though in the region of the angle the trabeculae become somewhat opened out. The coronoid is a muscular process whose density depends on the strength of the temporal muscle, and similarly the density of the angle depends on the mass of the medial pterygoid and masseter. These last muscles, it is said (Walkhoff, 1922), produce a series of trabeculae which radiate from the neighbourhood of the last molar tooth to the region of the angle on the inner side. These trabeculae, known as the trajectorium radiatum, have come to be regarded as distinctive of the anthropoid jaw.

If X-ray pictures of anthropoid and human jaws are examined it is possible to follow the upper and lower trabecular trajectories as they diverge from the condyle and pass along the upper and lower borders of the body of the jaw. The departures from the compact arrangement due to teeth and muscular processes have been mentioned. The loose mesh of trabeculae passing between these trajectoria can be seen, and the neutral zone indicated by this open mesh can be followed right up to the condyle. The inferior alveolar canal naturally occupies the interior of the neutral zone. This general pattern can be made out in the human, the anthropoid, and in the monkey jaw.

Walkhoff regards the junction of the body and ascending ramus as a place of weakness, and states that its reinforcement is achieved differently in the orang, the gorilla, and man. In the orang increased strength is got by the development of the trajectorium radiatum, a system of trabeculae radiating from the region of the last molar tooth, crossing the neutral zone, and diverging on the inner aspect of the angle. In the gorilla there is no system of such radiating trabeculae, but the junction is guarded by the development of compact bone on the inner aspect of the angle of the jaw and throughout the coronoid process. In man the trajectorium radiatum exists only in its apical portion about the last molar tooth. It cannot be traced further, and is replaced about the inner aspect of the angle by compact bone.

These three ways of strengthening the junction of the body and ramus are so distinctive that in the case of the gorilla, says Walkhoff, inspection of this region alone is sufficient for identification. Our own studies of a large number of primate jaws, including many monkeys, several of each of the anthropoid apes, and a great many human, have brought us to the conclusion that Walkhoff has rather exaggerated these architectural differences in the formation of the jaw at the junction of the body and ascending ramus. Rather it seems to us that at this place in all jaws a feeble system of trabeculae, crossing from the last molar tooth region to the angle, can be made out. Usually, however, these are not sufficiently condensed to separate them from the general meshwork of trabeculae. The only possible exception is the formation of the trabeculae in

this region in some old male anthropoids, especially the orang. Walkhoff has a picture of such a one that justifies his statement for this type. We believe then that there are no characteristic differences to be found in this region, either in the anthropoids or man. Neither the trajectorium radiatum nor the disposition of compact bone in this region has any distinctive value. (See Pl. I, figs. 4, 5, 6.)

There is, however, an effect on the internal architecture due to the increasing curvature of the neutral zone observed as one passes from the anthropoid to the human jaw. It has been stated that the upper and lower trajectoria and the neutral region between them converge in the condyle. This neutral region bears the alveolar canal with the nerves, blood vessels, etc. The neutral region and its contained bony canal run together and are quite congruent in their alignment so long as the fundamental horizontal arrangement of ramus and body is not departed from. The jaw of man still shows the fundamental architectural plan, but the curvature of the neutral region has produced certain changes. The dorsal end of the alveolar canal forms an angle with the neutral zone. The latter continues backwards towards the condyle, while the former passes more directly upwards. Further the increased curvature of the neutral zone in man carries the alveolar canal well below the roots of the molar teeth. In the anthropoids the alveolar canal is much straighter and impinges upon the roots of the last molar tooth. The neutral zone, or rather the zero position, where tension changes to compression is nearer the lower border of the jaw in man.

A very good X-ray picture of the Piltdown jaw has been published by Underwood (1913). When this is compared with that of the chimpanzee jaw it is obvious that there is the closest similarity. In both the alveolar canal is straight, close to the molar teeth, and in direct alignment with the neutral zone which obviously proceeds towards the condyle. The body of the Piltdown jaw is more slender, and its teeth project more above the alveolar margin than in the chimpanzee. Otherwise the internal pattern is the same (cf. Keith, 1929). Indeed for the ascending ramus the details are remarkably similar.

We conclude therefore that there is no distinctive human or anthropoid internal architecture of the lower jaw. Each conforms in the arrangement of its trabeculae to what might be expected from a study of the external features. The anthropoid jaw preserves more clearly the fundamental horizontal plan of the jaw, while in the human there is some departure from this, producing change in the alignment of the neutral zone with the alveolar canal. The internal architecture of any bone being a reflection of its outer form and of its function in no way affects whatever genetic conclusions have been drawn from its external anatomy.

Keith (1929) makes reference to the change in the curvature of the inferior alveolar canal in man and compares it with that of the great apes. Gregory (1934) devoted a subsection of his book to the same feature. He insisted that if the condyle of the jaw is in the same line as the teeth there could be no down-bending of the face. This is the condition, he stated, in primitive insectivorous

lemuroids and *Tarsius*. In the anthropoid apes and man there is of course down-bending of the face. This difference of the higher from the lower primates is in accord with the general thesis of his book.

Reference to the radiogram of *Tarsius* (Pl. I, fig. 1) reveal that the jaw has quite a considerable degree of curvature in its neutral zone recognizable by its clearness wherein lies the inferior alveolar canal. The usefulness of the radiographic method is here shown by the fact that it uncovers the true alignment of the jaw and corrects the misleading conclusions that might be drawn from the size of the muscular processes. Furthermore, reference to Pl. I, ignoring actual size of the mandible, suggests that the alignment of the neutral zone and alveolar canal in *Tarsius* (fig. 1), *Macaca* (fig. 2) and man (fig. 3) forms a series in which the members agree with one another more than they do with any member of the series formed by the orang (fig. 4), chimpanzee (fig. 5) and the gorilla (fig. 6). We may then perhaps also conclude that man in the curvature of the neutral zone and alveolar canal of his jaw develops an early primate feature.

CONCLUSIONS

1. In Primate jaws there is a general uniformity in the internal architecture. This internal architecture is consistent with the external form of the jaw.

2. There are no qualitative aspects of the internal architecture which have a diagnostic value for the great apes or man.

3. The study of the internal architecture of the jaw suggests that elevation of the condyle above the teeth, or down-bending of the face or curvature of the neutral zone and alveolar canal is a primitive Primate character.

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EXPLANATION OF PLATE I

Each of the Figs. 1 to 6 is a radiogram of the mandible.

Fig. 1. *Tarsius* spectrum. The clear, curved neutral zone is seen bending upwards towards the condyle from between the thin trajectorium dentale and the trajectorium basilare of the body of the jaw. With the contained alveolar canal it lies well below the teeth. The angular process is large. ×414.

Fig. 2. *Macacus rhesus*. The neutral zone extends upwards into the condyle. Below as it turns to reach the body the last molar tooth reaches almost to the alveolar canal. Nat. size.

Fig. 3. *Homo sapiens*. The neutral zone and the alveolar canal both lie well below the teeth. In the ascending ramus the neutral zone is directed towards the condyle and the alveolar canal towards the coronoid notch. Nat. size.

Fig. 4. Orang. The neutral zone is even straighter than in the chimpanzee. The last molar tooth impinges upon it and the alveolar canal. Nat. size.

Fig. 5. Chimpanzee. The neutral zone is much less curved; it extends into the condyle and along with the canal lies much closer to the teeth. Nat. size.

Fig. 6. Gorilla. The condition of the neutral zone and alveolar canal closely resembles that of the two preceding. Nat. size.

Fig. 1.

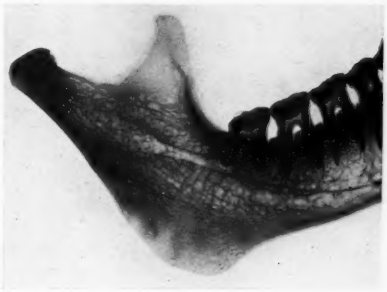

Fig. 4.

Fig. 2.

Fig. 5.

Fig. 3.

Fig. 6.

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A CASE OF AN UNUSUAL ARRANGEMENT OF THE GUT

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The case to be described here was found by the students dissecting the abdomen who noticed the abnormal position of the caecum and the appendix. They reported the matter to Prof. D. E. Derry, who charged me with the task of investigating the case.

The subject was a 60 years old hospital patient who died of pulmonary tuberculosis. A few other anomalies have been met with in the course of dissection which will be referred to later.

The drawing (Fig. 3) was made with the caecum and appendix in their undisturbed position, but the small intestines (*S.int.*) have been pulled to the right and the greater omentum upwards. We can clearly see that the caecum and appendix are placed on the left side and that the appendix is terminal in position, as can be gathered from the continuity of the taeniae coli over it. The mesoappendix is well marked, and the ileum is seen passing behind it to join the caecum. An ileo-caecal fold passing transversely and lying behind the mesoappendix also is marked (*Il.cae.f.*).

From the caecum the large bowel is continued to the right and slightly upwards. It then bends on itself, turning to the left to form the transverse colon. Reaching the left side it descends, forming the descending colon (*Des.col.*). The upper of the two pointers which mark it indicates the beginning of a loop of descending colon which reaches as far as the aorta and is here hidden from view. The termination of this loop is indicated by the lower pointer marked (*Des.col.*). There is another coil of descending colon partly hidden by caecum and appendix, from behind which the pelvic colon (*Pel.-col.*) is seen to run to the true pelvis. It is necessary to refer here to Fig. 1 which represents the axis of the main part of the large intestine. The two loops of the descending colon can be gathered from the diagram (Fig. 1) and the part marked ◊ ◊ of the upper loop is firmly attached by adhesions to the adjacent part of caecum and large bowel but mainly to the latter. These adhesions are so strong that they keep the parts in place even after the dissection.

As to the blood supply of the part of the large intestine which is described here, we may mention that the inferior mesenteric artery supplies the lower loop of descending colon, while opposite *A* in Fig. 1 ends a branch of the superior mesenteric artery which joins a branch of the inferior mesenteric. Two branches arise from the left side of the superior mesenteric artery and

supply alone the large bowel between *A* and the appendix as well as part of the ileum. Fig. 2 helps to explain the condition. The inferior mesenteric vein joins the superior mesenteric vein instead of the splenic vein.

It should be noted that the attached border of the mesentery of the small intestine lies altogether to the right of the middle line, and perhaps it is not out of place to point out that the mesentery of the caecum and adjacent part of the large intestine is in continuity with the mesentery of the small intestine.

The oesophagus leads to the stomach which has the normal relations of the stomach bed, but is of a peculiar tubular shape. It ends at the pylorus marked by the sphincter verified by dissection. The duodenum has a short first part attached to the liver by a part of the lesser omentum. This part

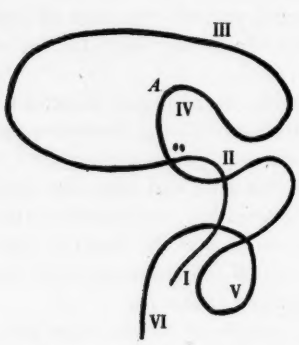

Fig. 1.

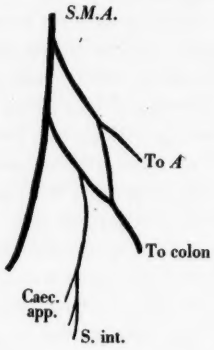

Fig. 2.

Fig. 1. Drawing to represent the axis of the large bowel starting from appendix at I, on to caecum at II, transverse colon at III, upper loop of descending colon at IV, lower loop o same at V, and pelvic colon at VI.

Fig. 2. Scheme to represent the arterial supply of large intestine. *S.M.A.* superior mesenteric artery.

has a tendency to be directed backwards towards the neck of the gall bladder. The duodenum next descends almost downwards, receives the bile duct joined by the pancreatic duct, thus marking the end of the foregut from the embryological point of view. The midgut starts at this point, and the gut is directed upwards and slightly backwards, forming a U-shaped loop with the part lying on its left. The pancreas makes its appearance between the two limbs in the undisturbed specimen. The transverse part of the gut which lies to the right of the loop is continued into the right limb of the loop through the medium of another loop which is fixed in place, and lies most posteriorly. Its apex is considered to be the duodeno-jejunal junction.

The pancreas can be seen projecting as far as the ascending limb of the duodenal loop, and it also lies behind it. The bile duct grooves the pancreas as it lies along the descending limb of the loop, and just before it enters the

gut it is joined by the pancreatic duct. There is no accessory pancreatic duct along the descending limb of the duodenum. The arteries of the foregut are normal in position and distribution, but the superior pancreatico-duodenal branch of the gastro-duodenal artery supplies the descending limb and half of the ascending limb of the duodenal loop, and so does coincide with the opening of the bile duct which is considered as the limit of the foregut.

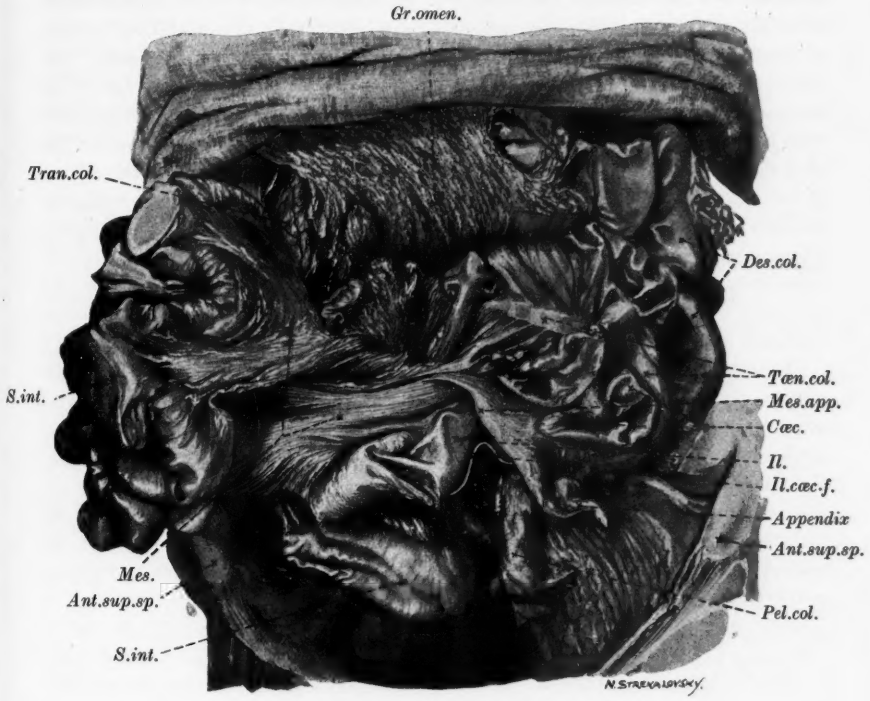

Fig. 3. To show the position of caecum on left side. The coils of small intestines have been pushed to the right and upwards.

EMBRYOLOGY

Before discussing the nature of this unusual arrangement we may give a brief account of the known embryological facts. Frazer divides the process of development of the gut into four stages, in the first of which there is no extra-abdominal gut beyond the yolk sac and the vitello-intestinal duct. In the second stage the gut lies mostly in the umbilical sac, in the third the gut returns to the abdomen and gets disposed therein, and in the fourth the parts get ultimately fixed in position. The proximal limb of the loop lies to the right of the distal limb in the umbilical sac, and the two limbs of the loop where

they become continuous with the upper and lower parts of the rest of the tube are relatively fixed by thick areas of mesentery, duodenal and colic.

The conditions present before the intestinal coils enter the abdomen are:

(1) Dorsoventral septum of abdominal colon and mesocolon.

(2) There is above this a duodeno-pancreatic mass on the right and an omental bursa and stomach on the left. A large liver fills up on each side the remainder of the cavity of the abdomen. By virtue of the relatively diminished intra-abdominal pressure the umbilical gut returns to the abdomen at the 40 mm. stage. This return is sudden and complete but not *en masse*, the caecum being retained in the sac because of its size and returns last. The cranial limb of the loop entering first pushes the septum of colon and mesocolon over to the left, and the coils pass to the left below the continuity between the abdominal colon and the part still in the sac. The immediate result of the return of the colon (40–45 mm.) is that it lies on the coils of small intestine with the caecum wedged in between these coils and the liver near the middle line. Within a few days the caecum has found its way behind the right edge of the mass of coils, the colon leading to it being straightened out over the neck of the mesentery of the coils. At the 63 mm. stage it is in contact with the dorsal wall just above the iliac crest.

Lastly, the various parts of the intestinal tract, having reached their proper planes, extend in these planes to reach their definitive positions and acquire secondary adhesions to neighbouring surfaces which fix them in these positions. The obliquely directed attached border of the mesentery is really the extreme left limit of the area of adhesion of the mesocolon of the loop. The curve of the duodenum has nothing to do with the return of rotation of the intestine, but owes its presence primarily to the growth of the head of the pancreas in the mesoduodenum pushing the duodenum to the right and giving it the usual curve before the bowel enters the abdomen.

EXPLANATION

In the light of this knowledge this particular case can be explained. The pancreas growing in the dorsal mesoduodenum pushed the duodenum to the right, and as it happened that its distal end which is the proximal limit of the upper limb of the loop was not fixed, it was also pushed to the right of the middle line, and so the duodenum did not acquire its C-shaped arrangement, and the duodeno-jejunal flexure started on the right instead of the left of the middle line. The caecum on its return was not far from the middle line and lay close to the rest of the colon before that was pushed far to the left. The adhesions which bind the descending colon to the part of the large intestine just beyond the caecum must have developed at that stage and dragged the caecum and adjoining part to the left. Between that part and the beginning of the descending colon the growth has led to the development of the loop described above, starting from the caecum, going to the right and then turning to the left to form the transverse colon.

Three human embryos in the middle third of the third month, were examined, and all show that the mesentery of the small intestine is not yet fixed along the usual oblique line. The caecum and colon lie above the coils and between them and the liver. As to the reversed line of the attachment of the mesentery, Frazer believes that it is the left-hand limit of the mesocolon of the loop, and as the caecum and colon lie to the left in this case and also the duodeno-jejunal flexure starts on the right of the middle line, it naturally happens that the line of attachment must lie to the right and represents the right-hand limit of the mesocolon of the loop. The terminal appendix is a foetal phenomenon due to lack of development of caecal diverticula which in the ordinary course of events make the position of the appendix assymmetrical.

OTHER ANOMALIES

These were found in the same subject in the course of dissecting the other parts. They are:

(1) A lateral branch of the first intercostal nerve replacing in part the medial cutaneous nerve of the arm.

(2) The descending hypoglossal nerve arises on the left side from the vagus nerve.

(3) The median nerve crosses deep to the brachial artery on the right side. This means that the superficial brachial artery persisted in that arm and replaced the original brachial artery.

(4) On the left side the median nerve passes between the radial and ulnar arteries into which the brachial has divided in the arm. This means that both superficial and proper brachial have persisted.

SUMMARY

The duodenum does not exhibit its usual shape, the jejunum starts on the right of the middle line, the caecum and appendix lie on the left, the appendix is terminal and the oblique line of mesenteric attachment starts from the right in the vicinity of the kidney and is directed downwards and to the left as far as the middle line. A short account of the embryological facts is given and an attempt is made to explain the case in the light of these facts.

I wish to thank Prof. D. E. Derry for his suggestion to investigate the case and for his valuable help. I am indebted to Mr N. Strekolovsky, the Faculty artist, for the drawings.

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CONCERNING THE DEVELOPMENT OF THE PRECHORDAL PORTION OF THE VERTEBRATE HEAD

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It has been suggested by an eminent authority that I give, with suitable figures in illustration, an account of my present views regarding the development of the prechordal portion of the vertebrate head. This requires, first, a careful reconsideration of the conditions in the Plagiostomi and then consideration of those in the Holocephali, Cyclostomata and Ganoidei, and it may be here stated that I am now able to give an explanation of the somewhat puzzling manner in which the hypophysis develops in the latter fishes. The conditions in the Teleostei, Dipnoi and Amphibia are not particularly considered. The drawings for the figures were prepared by Gen. G. Wannovsky.

PLAGIOSTOMI

In early embryos of *Acanthias* the alimentary canal is said by Platt (1891) to fill completely the head region. The neural plate lies flat on the dorsal surface of the egg and does not extend forward quite to the anterior end of the alimentary canal.

In a 2·7 mm. embryo of *Acanthias* the neural groove is well developed, as shown in the accompanying Fig. 1, which is a copy of Scammon's (1911) Fig. 3 giving a median view of an approximately bisected embryo. The groove lies directly upon the underlying portion of the alimentary canal and presents anterior and posterior sections which lie at a considerable angle to each other. The posterior section begins in the branchial region and from there the median line of its internal surface extends antero-ventrally in a smooth and even curve to the hind end of the premandibular (preoral) gut, where the anterior section begins and extends anteriorly slightly beyond the tip of the latter gut. The infundibular process of the brain develops at the angle between these two sections and accordingly lies approximately, if not actually, in the intersegmental line between the mandibular and premandibular sections of the alimentary canal. The anterior section of the groove is thus definitely premandibular in position in so far as its relations to the alimentary canal are concerned, and accordingly may be referred to for descriptive purposes as the premandibular section of the groove, and that part of the floor of the brain that is developed in relation to it may be referred to as the premandibular section of that floor. The optic chiasma is said by Platt to develop in this

premandibular section of the groove and the recessus preopticus to lie approximately dorsal to the tip of the premandibular gut. The premandibular gut has the appearance of being a diverticulum projecting anteriorly from the anterior wall of the foregut immediately above its floor, and I have heretofore considered this to have been due to compression caused by the sinking inward of the neural groove, and as it is the infundibular portion of the groove that sinks deepest into the underlying tissues I have referred to it as the descent of the infundibulum. Scammon, however, says (1911) that in a 2 mm. embryo of this fish the preoral gut is almost square in cross-section, and Platt refers to it as tubular in shape, neither of which is favourable to a marked dorso-ventral compression of this part of the gut. It therefore seems probable that the conditions here are due to arrested development of the premandibular section of the alimentary canal and not especially to downward compression.

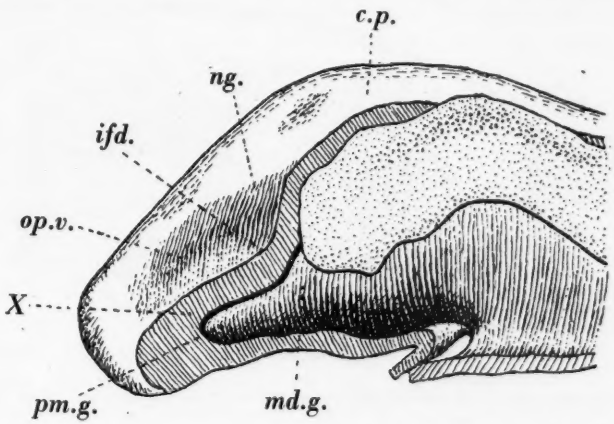

Fig. 1. Median view of the bisected head of a 2·7 mm. *Acanthias* embryo. After Scammon.

That part of the neural groove that lay directly upon the dorsal surface of the premandibular portion of the alimentary canal would then have simply sunk inward as that part of the canal became reduced in relative diameter and have pulled the posterior portion of the groove downward after it.

The point *X* shown in the figure is assumed to lie in the line between the ectoderm covering the anterior surface of the brain and that covering the anterior surface of the premandibular visceral segment, and hence approximately ventral to the recessus preopticus. These relations of the point *X* to the cranial and visceral ectoderm suggest that it represents the tip of the later to be developed Rathke's pocket, for that tip lies approximately between those two ectodermal surfaces, as will be explained when later describing a 7 mm. embryo. The tip of the pocket, however, lies in the latter embryo approximately external (ventral) to the hind end of the infundibulum, the external opening of the pocket lying external (ventral) to the recessus preopticus, the outer surface of the brain

between these two points being covered with cranial ectoderm. The brain of the 2·7 mm. embryo must accordingly in older embryos have shifted forward relatively to the premandibular visceral segment until the hind end of the infundibulum has come to lie dorsal to the point *X*. The ectoderm that in this 2·7 mm. embryo covers the anterior and ventral surfaces of the premandibular segment would then correspond to the buccopharyngeal upper lip of older embryos together with the primarily dorsal wall of Rathke's pocket, as will be evident when older embryos are described. There are thus on the strongly curved anterior end of the head of this embryo the following several regions arranged successively from above downward; forebrain, neuropore with related olfactory placodes, tip of Rathke's pocket, buccopharyngeal upper lip and the place of the future buccopharyngeal plate, and it will be

Fig. 2. Median view of the bisected head of a 3·5 mm. *Acanthias* embryo. After Scammon.

later shown that in early embryos of the Ganoidei these same regions occur successively in the same order but on a much less strongly curved surface.

In a 3·5 mm. embryo of *Acanthias* the brain has shifted forward to a considerable extent relative to the alimentary canal, as shown in the accompanying Fig. 2 which is a copy of Scammon's Fig. 6 giving a median view of an approximately bisected embryo. In connexion with this shifting forward of the brain the premandibular gut has been withdrawn from the space it previously occupied immediately beneath the premandibular section of the neural groove, the tip of this space lying ventral to the hind edge of the optic chiasma instead of lying slightly anterior to the chiasma beneath the preoptic recess. The point now occupied by what will later become the tip of Rathke's pocket cannot be recognized, but it must lie approximately beneath the optic chiasma and by the further shifting forward of the brain it will ultimately come to lie beneath the infundibulum. The space previously occupied by the premandibular gut is now shown filled with premandibular mesoderm. This

space is relatively small, and the dorsal and ventral ends of the band of mesodermal tissue on either side of the head in which the related premandibular branchial bar will later develop are relatively close to each other, the band quite certainly being slightly curved in form, the outer end of the curve directed somewhat anteriorly because of the rounded shape of the anterior end of the alimentary chamber. The floor of the premandibular gut is still practically on the level of that of the mandibular and more posterior portions of the alimentary canal, for these latter portions of the canal have not yet begun to expand ventrally as they do in older embryos. The floor of the mandibular section of the canal which will later become the internal layer of the buccopharyngeal plate is accordingly still in a nearly horizontal position and has not yet come into contact with the ectoderm immediately external to it.

In a 7 mm. embryo of *Acanthias* the neural groove has shifted relatively so far forward that the hind end of the infundibulum lies approximately directly internal (dorsal) to that point of the ectoderm that will later become the tip of Rathke's pocket, as shown in Fig. 3 which is a copy of one of de Beer's figures (1926, Fig. 85). What I have called the premandibular section of the neural groove is now completely lined externally with cranial ectoderm, and owing to the marked expansion of the forebrain the anterior portion of the head back to and including the premandibular section of the neural groove has swung downward and backward around a horizontal axis passing approximately through the future tip of Rathke's pocket to such an extent that this cranial ectodermal surface is presented almost directly posteriorly. Between this posteriorly directed cranial surface and the ectoderm covering the anterior portion of the ventral surface of the branchial chamber there is accordingly a large and approximately right angle. This large angle which will later become the Kieferaugenspalte of Haller's (1923) descriptions of older embryos may be called the hypophysial fold, the tip of the fold forming the future tip of Rathke's pocket. The mandibular and more posterior portions of the alimentary canal have begun to expand ventrally, this pressing the floor of the mandibular section of the canal downward and forward into a slightly anterodorsally directed position. The premandibular gut is not particularly described by de Beer and cannot be identified in his figure; it is, however, shown by Haller in a median section of a 4·5 mm. embryo of *Raia* as a small pointed process projecting forward from the dorso-anterior corner of the gut. It is embedded in a mass of cells that lies immediately internal to the dorso-posterior wall of the hypophysial fold, and that part of this mass of cells that

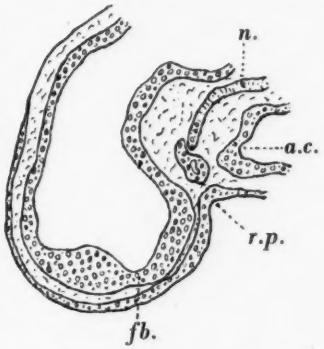

Fig. 3. Median sagittal section of a 7 mm. embryo of *Squalus*. After de Beer.

immediately surrounds the process later disappears excepting only a narrow strand the ultimate fate of which Haller could not determine. This little process of the gut is currently called Sessel's pocket and its present position near the dorsal instead of the ventral edge of the mandibular gut is not the result of actual shifting of its position relative to that gut, but to the marked expansion ventrally of the mandibular and more posterior portions of the alimentary canal. The mandibular gut has actually no anterior surface excepting that represented by the line of contact with the hind edge of the premandibular gut, its exposed surfaces being either dorsal, lateral or ventral, the latter surface being perforated by the buccopharyngeal (oral) opening.

In an 8 mm. embryo of *Raia* described by Haller the anterior end of the

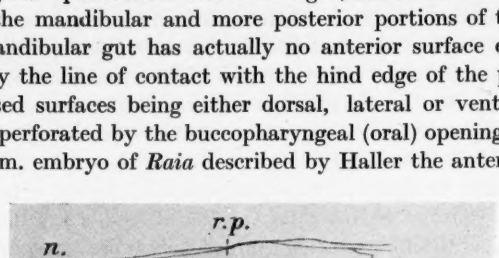

Fig. 4. Median section through the head of an 8 mm. embryo of *Raia clavata*. After Haller. Reversed in direction.

head has swung downward, backward and upward to such an extent that the two walls of the hypophysial fold have come together on either side of the median line and there completely fused with each other, as shown in the accompanying Fig. 4 which is a copy of one of Haller's figures (1923, Fig. 1). These two surfaces of fusion extend from the transverse line of the hind end of the infundibulum to a point approximately in the transverse line of the preoptic recess, this indicating the full depth of the hypophysial fold. A median space called Rathke's pocket is thus cut out of the latter fold, the depth of the pocket, like that of the fold, corresponding approximately to the length of what I have called the premandibular section of the floor of the brain, the pocket lying directly external to this section of the brain. What at this stage of development is the anteroventral wall of the pocket is thus of cranial ectoderm, the posterodorsal wall

being of visceral ectoderm and quite certainly derived from the anterior portion of the ectoderm that in early embryos covers the anterior and ventral surfaces of the preoral gut. At the external opening of Rathke's pocket the median longitudinal line of the latter ectoderm turns abruptly dorsally and becomes continuous with the mandibular ectoderm that forms the dorso-anterior border of the buccopharyngeal opening. This part of the line of ectoderm is thus largely of premandibular origin but partly of mandibular origin, and it forms the external lining of what Haller calls in a 20 mm. *Acanthias*, described immediately below, the transverse hypophysial bolster. In the 8 mm. embryo of *Raia* the mandibular arch is said to show subdivision into four segments which are called by Haller from above downward, the Kieferaugenspaltstück, Oberkieferstück, Zwischenstück and Unterkieferstück. The Kieferaugenspaltstück is said to be the pharyngeal element of the arch and it is definitely said to take no part in the formation of the upper jaw and some part of it is just as definitely said to form the floor and lateral walls of the pituitary fossa, this fossa being referred to by Haller as the posterior portion of the large Hirnbodenbucht peculiar to these fishes. The mandibular arch is considered by him to consist of two portions, one of which he calls the postorbital or primitive arch, the other portion being said to be of secondary origin and being called the suborbital portion of the arch. The larger portion, or body, of the Kieferaugenspaltstück is said to form the dorsal end of the primitive arch, the suborbital portion of the arch and the anterior end of the palatoquadrate (Oberkieferstück) being developed from an anterior process of the Kieferaugenspaltstück. This will be further explained when considering the conditions in 20 and 30 mm. embryos of *Acanthias* immediately below.

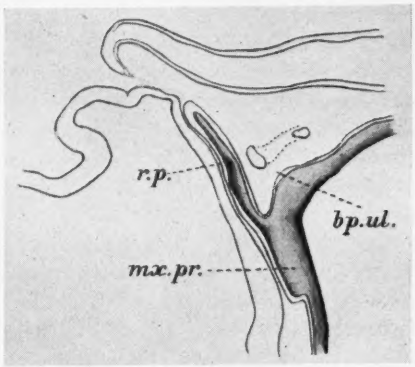

Fig. 5. Median section through the hypophysial region of a 20 mm. embryo of *Acanthias*. After Haller. Reversed in direction.

In a 20 mm. embryo of *Acanthias* the cranial flexure has begun to be reduced by the swinging forward and upward of the anterior end of the head, but the horizontal axis around which this takes place has shifted from the tip of Rathke's pocket to a point approximately through the external opening of that pocket, as shown in the accompanying Fig. 5 which is copied from Haller's Fig. 4. This shifting of the axis of rotation is due to the marked shortening in length of the ventral surface of this part of the head resulting from the infolding of the hypophysial fold and it is equal in amount to twice the depth of that fold. The fold is in fact a pleat taken in the ectoderm covering the

ventral surface of the head and projecting anterodorsally into the substance of the head. There has been no corresponding shortening in the length of the floor of the brain and because of the change in the axis of rotation, both what I have called the premandibular portion of the latter floor and Rathke's pocket swing backward and downward as the remaining part of the anterior end of the head swings forward and upward. The hind end of the infundibulum is connected with the ventral end of the anterior limb of the plica encephali ventralis, and as the infundibulum swings backward and downward it carries with it the ventral end of that limb of the plica until they both reach their adult positions approximately ventral to the anterior end of the medulla oblongata. The so-called maxillary processes, one on either side of the head, are

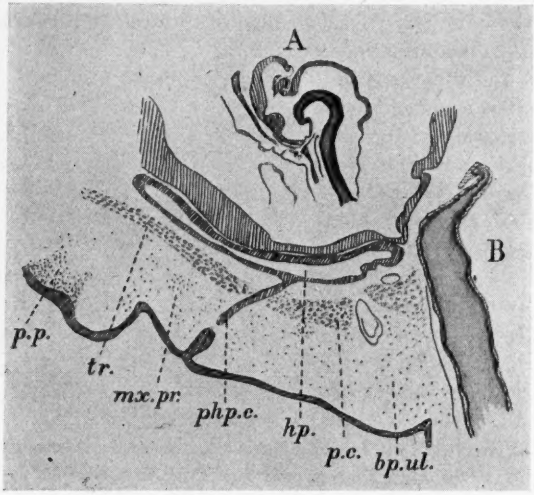

Fig. 6. A. Median section through the head of a 30 mm. embryo of *Acanthias*. B. Enlarged view of the hypophysial region in the same embryo. After Haller. Reversed in direction.

said to grow forward from the anterior surface of the transverse hypophysial bolster, and they appear as horizontal ridges directed morphologically ventrally from the ventral surface of the anterior portion of the head. They are said to extend forward to the so-called lachrymal groove where each turns mesially and meets and fuses in the median line with its fellow of the opposite side. A prehypophysial recess bounded posteriorly by the hypophysial bolster and opening ventrally to the exterior is thus formed on the ventral surface of the head, Rathke's pocket opening into it at its morphologically dorsoposterior edge. Haller says that at this stage there is no mesodermal tissue in either of these maxillary processes.

In a 30 mm. embryo of *Acanthias* the hypophysial bolster above referred to, which I have called in an earlier work (Allis, 1932*a*) the buccopharyngeal

upper lip, has grown forward to such an extent that its morphologically ventral surface reaches nearly to the hind edge of a group of cells that will later become the palatine process of the palatoquadrate, as shown in the accompanying Fig. 6 which is a copy of Haller's Fig. 5. The ventral edges of the maxillary processes have grown mesially and met and fused with each other in the median line. At the same time the mesial walls of the processes meet and fuse with each other in the median plane and break down and completely disappear excepting only certain parts that are preserved to form the anterior and lateral walls of the prehypophysial canal and probably also the enclosing walls of an anterior prolongation of the hypophysis which extends forward from Rathke's pocket along the ventral surface of the brain. The hind wall of the prehypophysial canal is formed by the anterior surface of the hypophysial bolster and is accordingly of visceral ectoderm, its anterior wall being of cranial ectoderm, the canal extending forward from the external opening of Rathke's pocket and opening into the buccal cavity slightly posterior to the palatine processes. Slightly ventral to the anterior prolongation of the hypophysis and extending forward slightly beyond its tip there is a long band of mesodermal cells separated into two parts by the prehypophysial canal. The two parts of this band are called by Haller the anterior and posterior trabeculae and are evidently, respectively, the trabecular and polar cartilages of current descriptions of the adults of these fishes. The polar cartilage lies wholly in the hypophysial bolster and is considered by Haller to represent the body of the Kieferaugenspaltstück and is accordingly quite certainly the entire pharyngomandibular. Ventral to the anterior end of the trabecula there is a group of mesodermal cells that is said by Haller to represent the anterior end of the palatoquadrate (Oberkieferstück) and this group of cells together with those that form the trabecula form what Haller calls the suborbital portion of the mandibular arch and are considered by him to have both been derived from a process of the Kieferaugenspaltstück of its side of the head.

From this careful reconsideration of the conditions in these fishes I am convinced that, in them, the hypophysis is formed by the folding together of two ectodermal surfaces that cover at this stage of development the one a cranial and the other a visceral surface, that it is accordingly in no sense either an ingrowth or an invagination, and that it is also in no sense what de Beer calls an overgrowth, for in all of the embryos considered it always has approximately the length of what I have called the premandibular section of the floor of the brain, that is that part of that floor that extends approximately from the hind end of the infundibulum to the preoptic recess. Furthermore, I see no reason to change my opinion expressed in 1931 and 1932 that the polar cartilage is the pharyngeal element of the mandibular bar and the trabecular and palatine cartilages, respectively, the dorsal and ventral halves of the premandibular branchial bar, and I have attempted to show in the accompanying purely diagrammatic Fig. 7 the manner in which they have come to be developed from those branchial bars. This figure shows only the anterior

portion of the alimentary canal and the premandibular, mandibular and hyal branchial bars. It is intended to present four successive stages in the progressive abortion of the premandibular section of the alimentary canal and the related changes in the shape and position of the mandibular and premandibular branchial bars. In the first stage shown the premandibular section of the canal is assumed to be of the same size as the posterior sections. In the second stage the premandibular section has already diminished considerably in relative size and the more posterior sections have expanded slightly dorsally. In the third stage the posterior sections of the canal expand ventrally and the premandibular branchial bar has become entirely independent of the related section of the canal, and the articular joint between the pharyngeal and epal elements of the mandibular arch lies opposite the closely adjoining dorsal and ventral ends of the premandibular bar. In the last stage the premandibular section of the alimentary canal has entirely disappeared and the dorsal and ventral halves of the premandibular branchial bar are in position to fuse, respectively, with the ventral end of the pharyngomandibular and the dorsal end of the epimandibular and so become the trabecular and palatine cartilages.

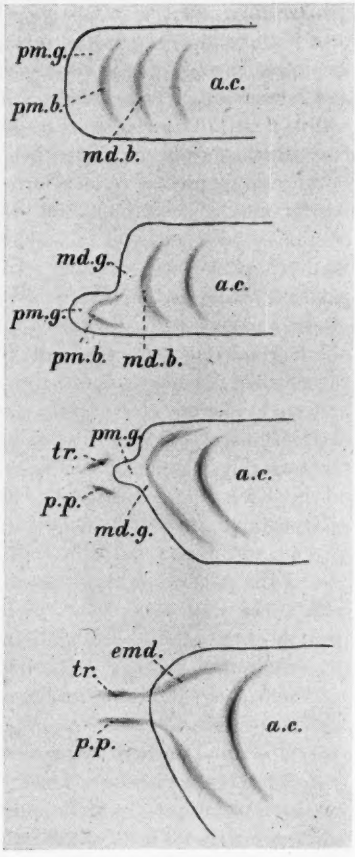

Fig. 7. Diagrammatic figure to show the manner of development of the trabecular, polar and palatine cartilages.

De Beer (1931*b*) considers the manner of development of the polar, trabecular and palatine cartilages as set forth in my earlier works to be based on purely morphological considerations and hence open to question. He accordingly attempted in 1931 to trace in *Scyllium*, as Haller had already done in *Acanthias* and *Raia*, the cells that enter into the composition of these several cartilages directly to them from their points of origin. A group of cells is said by him to arise independently in each maxillary process without proliferation from adjacent regions. These cells, when they first appear, are said to be of uniform character and indistinguishably mixed with each other, but they soon separate into two groups, a superficial and a deeper

one. The deeper group is considered to be of premandibular origin, and the trabecula which develops in it is considered to represent either the entire branchial bar of the premandibular arch, or its larger dorsal portion, the ventral portion of the bar in the latter case breaking down and being dispersed. The superficial group fuses with the pterygoquadrate and becomes its palatine process, this process being nevertheless said to be a definite but secondary outgrowth of the pterygoquadrate and hence apparently being in de Beer's opinion of mandibular origin, although this is not definitely so stated. De Beer could not satisfactorily determine the origin of the polar cartilage, but he considers it probable that it is of mandibular origin. The pharyngo-mandibular is however considered by him to be quite probably represented in the little cartilage described by Sewertzoff & Diesler (1924) in the articular joint between the dorsal end of the orbital process of the palatoquadrate and the orbital wall, while both Haller and I considered this segment of the mandibular arch to have given origin to the polar cartilage. The conditions in *Scyllium* as thus described by de Beer would thus seem to be definitely favourable, rather than unfavourable, to my interpretation of the conditions in *Acanthias* and *Raia* as described by Haller. De Beer calls attention to the fact that as long ago as 1874 and 1875 Huxley contended that the trabeculo-polar bar, called by him simply the trabecula, forms a complete and single visceral arch. This, I regret to say, entirely escaped my notice when my earlier works relating to this subject were sent to press, and Haller does not refer to it. My work published in 1923 together with Haller's work published later in the same year would seem to have definitely confirmed Huxley's contention in so far as the visceral (branchial) origin of the bar is concerned, but if I am correct in my conclusion that this bar is formed by parts of two adjacent arches which fuse with each other, end to end, Huxley's conclusion that the bar represents a single and complete "visceral arch" is certainly not correct. De Beer, however, contends, as just above stated, that the trabecular part alone of the trabeculo-polar bar represents the entire premandibular branchial bar and he considers this to definitely confirm Huxley's view.

In embryos of the Plagiostomi older than those above considered the development of the prechordal part of the chondrocranium is best described by de Beer in a work entitled "The development of the skull of *Scyllium canicula*" (1931*a*). In a 34 mm. embryo of this fish the anterior ends of the trabeculae, curving mesially, have met and fused with the lateral edges of the hind end of a median cartilage which lies, at this stage, between the nasal sacs but later between the ventral edges of the nasal capsules. It is called by de Beer the rostral cartilage and is in no way an outgrowth of the trabeculae, the latter cartilages definitely ending, at this stage of development, approximately in the line between the orbital and ethmoidal regions, as they do in the 30 mm. embryo of *Acanthias* shown in Fig. 6. In a slightly earlier stage of *Scyllium* an ethmoidal process called by de Beer the lamina orbito-nasalis is said to extend laterally from the anterior end of the trabecula of its side of

the head, and somewhat later a planum antorbitale extends upward from it to form at the same time the hind wall of the nasal capsule and the anterior wall of the orbit. Mesial to the mesial edge of this planum another process called by de Beer the preoptic root of the orbital cartilage is said to grow upward from the anterior end of the trabecula and to meet and fuse dorsally with the orbital cartilage, so completing the dorsal and anterior boundaries of the orbit. An independent anterolateral wall to the nasal capsule has in the meantime developed, and the mesial wall of the latter capsule is then formed by a process that is said to grow upward and forward from the lateral edge of de Beer's so-called rostral cartilage near its hind end and meet and fuse with the dorsal edge of the anterior wall of the capsule. From this point of fusion the dorsolateral limb of the three-limbed rostral basket grows anteromesially and meets and fuses in the median line with the anterior end of its fellow of the opposite side and also with the anterior end of the ventromedian limb of the rostral basket which grows forward from the anterior end of de Beer's rostral cartilage. There is now, as soon as the mesial walls of the nasal capsules have been completed, a tall cavum internasale similar to that described by Gaupp (1906) in certain of the Amphibia excepting in that it is closed ventrally by de Beer's so-called rostral. Posteriorly it opens directly into the cranial cavity and anteriorly into the hollow of the three-limbed rostral basket, that basket having been considered by both Sewertzoff (1899) and myself to be the homologue of the cavum praecerebrale of the Notidanidae and Spinacidae. In a slightly older embryo, shown in the accompanying Fig. 8, still another process has been developed in this region, but the manner of its development in this fish is not here definitely given. It is, however, said (de Beer, 1931*b*) to correspond to two cartilages, one on either side of the head, developed in early embryos of *Rana* which are called the suprarostrals, each of them fusing with the anterior end of the corresponding trabecula. Stöhr (1882) is said to have considered these cartilages to be outgrowths of the trabeculae, but Spemann (1898) is said to have considered them to be of wholly independent origin. De Beer calls the single cartilage of *Scyllium* the suprarostral, but simply says of it that dorsal to his rostral process "a shorter and more blunt process extends forward between the median walls of the nasal capsules". He calls it in the

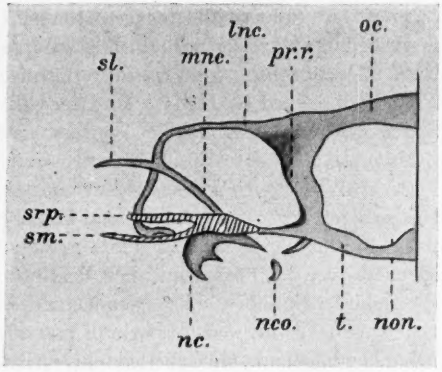

Fig. 8. Median view of the skull of a 45 mm. embryo of *Scyllium*. After de Beer. Reversed in direction. With index letters used by him.

text the suprarostral, but in the figure given of the bisected skull of an adult (Fig. 9) it is index lettered as the "Median wall of nasal capsule". It has the appearance in the figure of arising from the dorsal surface of de Beer's rostral cartilage approximately in the line of the anterior ends of the trabeculae. Running forward at about the middle of the height of the nasal capsules it cuts the cavum internasale into dorsal and ventral portions, the latter of which is thus cut off from the cranial cavity, but still retains its connexion with the cavum praecerebrale, while the dorsal portion retains its connexion with both these cavities. The origin of these several processes from the anterior ends of the trabeculae is evidently favourable to my conclusions that the ethmoidal

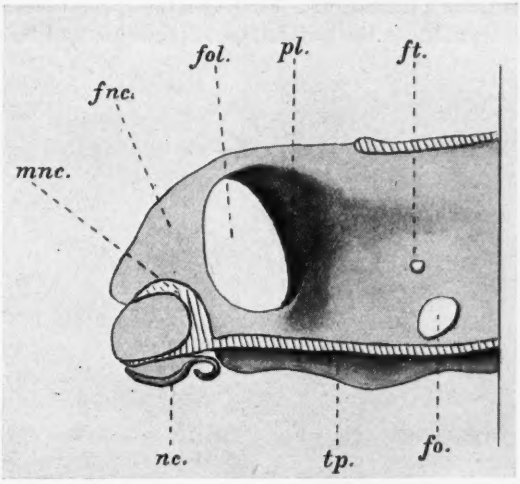

Fig. 9. Median view of the skull of an adult *Scyllium*. After de Beer. Reversed in direction. With index letters used by him.

region of the chondrocranium is of premandibular branchial bar or branchial-ray origin, the outer border of the antorbital wall being a branchial-ray bar the serial homologue of the branchial-ray bars of the mandibular and hyal arches which form, respectively, the lateral walls of the trigemino-facialis chamber and the hyomandibula of the Teleostomi (Allis, 1931*b*).

The so-called septum nasi of these fishes may now be considered, for there has been question of its relations to the trabeculae. That there is in *Scyllium* at no stage of development a median vertical internasal plate is evident from de Beer's descriptions of the development of this fish. There is, however, an internasal wall formed by the mesial walls of the nasal capsules together with the two median longitudinal processes called by de Beer the rostral and suprarostral and that ventral portion of the cavum internasale that lies between

the two latter processes. This internasal wall or so-called septum has also been described in others of those of the Selachii that possess a three-limbed rostral basket and that there was primarily in all of these septa a narrow median cavum internasale would seem to be established by what I described in an earlier work (Allis, 1913) as the apparently imperfectly chondrified condition of the median plane of the septum. This is well shown in Gegenbaur's (1872) and Parker's (1876) figures of median sections through the skulls of *Mustelus* and *Scyllium* which are reproduced in the accompanying Figs. 10 and 11. Comparing these two figures with each other and with de Beer's figure of a similar section through the head of an adult *Scyllium* reproduced in the accompanying Fig. 9, it is seen that there is marked difference in the names given by these three authors to the cartilages that bound or lie immediately anterior to the septum. In the Notidanidae, Spinacidae and Raiadae in which

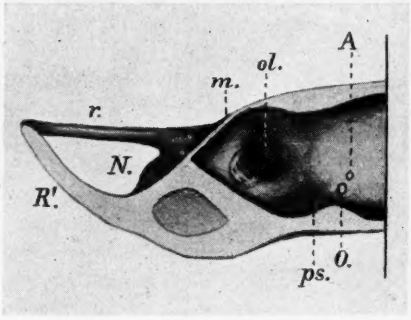

Fig. 10. Median section of the skull of an adult *Mustelus*. After Gegenbaur. Reversed in direction. With index letters used by him.

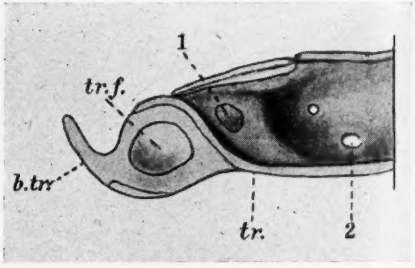

Fig. 11 Median view of the skull of an adult *Scyllium*. After Parker. Reversed in direction. With index letters used by him.

a septum nasi has never been described, so far as I can find, the trabeculae have heretofore been considered to fuse to form a trabecular plate, and this plate has been considered to be prolonged anteriorly to the end of the snout, the preorbital portion of the plate being called its rostral portion. This is typically shown in Gegenbaur's figure of a bisected skull of the adult *Acanthias*, reproduced in the accompanying Fig. 12 and also in Sewertzoff's (1899) figures of embryos of this same fish. On the ventral surface of the rostral portion of this continuous trabeculo-rostral plate Gegenbaur shows a median longitudinal ridge which he calls the median internasal ridge and designates in his figures by the letter *V*. This ridge is not shown in Sewertzoff's figures of embryos of this fish and would accordingly seem to be of later development. The nasal capsules of these fishes develop along the lateral edges of the rostral cartilage and project either lateroventrally or ventrally from those edges. This led me to conclude in an earlier work (Allis, 1917) that the internasal

septum of the Scylliidae and Carchariidae was developed as a result of a gradual shifting mesially of the capsules along the ventral surface of the trabeculorostral plate and their ultimate fusion in the median line with each other and also with the median ventral internasal ridge *V* of Gegenbaur's description, a portion of the median ridge being squeezed ventrally to form the ventral border of the septum. I, however, now consider the median ridge *V* to have been, in the Notidanidae and Spinacidae, primarily an independent cartilage that has fused with the overlying rostral portion of the continuous trabeculorostral plate and that in the Carchariidae and Scylliidae the nasal capsules have pressed these two bars apart and so come to lie between them. Gegenbaur in fact considers the ventral border of the septum to correspond to the median internasal ridge of his descriptions of *Acanthias* as shown by the use of the index letter *V* to indicate it in his figure of *Galeus* (1872, Pl. 5, Fig. 2). The dorsal border of the septum was therefore certainly considered by him to correspond to the rostral portion of the trabeculorostral plate of his descriptions of *Acanthias*, the septum accordingly lying ventral to the latter plate. Parker considers both edges of the septum to be anterior prolongations of the trabeculae, the septum accordingly being, in his opinion, intratrabecular in position. I, in my earlier works relating to this subject, have adopted the nomenclature employed by Gegenbaur and accordingly made the general statement that in these fishes the septum lies ventral to the trabeculae.

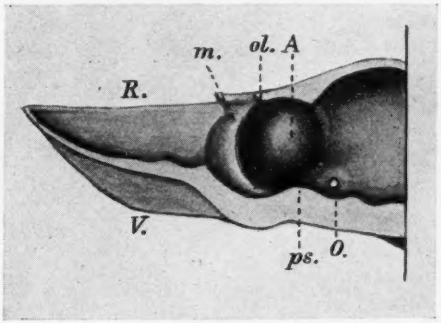

Fig. 12. Median view of the skull of an adult *Acanthias*. After Gegenbaur. Reversed in direction. With index letters used by him.

De Beer considers the ventral border, alone, of the septum to be the direct anterior prolongation of the trabeculae and hence maintains that the septum lies dorsal to the trabeculae, his opinion and mine, to which he takes marked exception, thus apparently differing simply because of a difference in the nomenclature employed and hence being of no particular morphological significance. If the ethmoidal region is largely of branchial-ray origin, as de Beer's descriptions of *Scyllium* would seem to indicate, the septum would in fact lie wholly anterior to the trabeculae and neither dorsal nor ventral to them.

HOLOCEPHALI

Schauinsland's (1903) figures of early embryos of *Callorhynchus* show definitely that the hypophysis of these fishes is developed in a manner strictly comparable to that in the Plagiostomi, and his figures of older embryos of *Callorhynchus* and my figure of a bisected skull of the adult *Chimaera colliei*,

reproduced in the accompanying Fig. 13, show just as definitely that the marked cranial flexure essential to this manner of development of the hypophysis has not later been completely reduced. This is evidently due to the development of a large vesicle called by Dean (1906) the frontal knob which presses upon the downturned anterior portion of the head and prevents its continued swinging upward and forward into its primitive position in the line prolonged of the axis of the body. This does not particularly affect the chordal portion of the skull and because of this the forebrain projects anteroventrally at a marked angle to the mid and hind brains and is relatively long. The eyeballs retain their normal positions immediately anterior to the otic region and

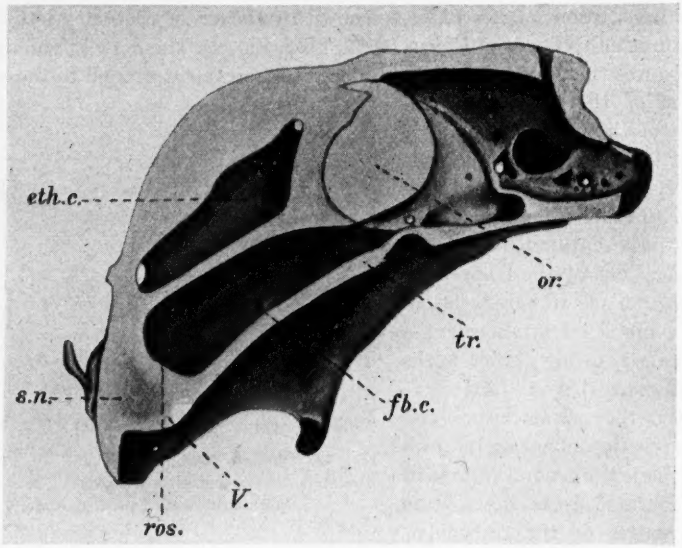

Fig. 13. Median view of the skull of an adult *Chimaera colliei*. After Allis.

hence lie dorsal to the hind end of the forebrain, the orbits being separated from each other by a thin median interorbital septum. The supraorbital cartilages form the dorsal borders of the orbits and hence lie at a considerable distance dorsal to the forebrain. The walls of the forebrain cavity must accordingly either be of cranial origin developed in relation to the membranous tissues that primarily enclosed the brain, or be upgrowths of the trabeculae that have met and fused with each other dorsal to the forebrain. Assuming that they were of trabecular origin, I suggested in 1926 that the trabeculae themselves had shifted upward lateral to the forebrain and reaching its dorsal surface had there met and fused with each other in the median line to form the roof of the forebrain cavity. There is no mechanical objection whatever to this assumption, for in early embryonic stages the trabeculae do not extend

forward beyond the orbits, as shown in the 30 mm. embryo of *Acanthias* (Fig. 6), and in shifting upward they would in no way have interfered with the connexion of the nervi olfactorii with the nasal sacs, as suggested by de Beer & Moy-Thomas (1935). The condition and position of the nasal septum however strongly suggests that the trabeculae actually form the floor of the forebrain cavity and the bounding walls of the septum, as they do in the Plagiostomi, for in my figure of *Chimaera*, published in 1917, the median plane of the septum is shown in the same imperfectly chondrified condition that it has in the Plagiostomi. This evidently indicates that the septum primarily enclosed within it the ventral portion of a cavum internasale. The dorsal portion of that cavum which, in the Plagiostomi, forms part of the cavum praecerebrale, would then probably be included in the so-called ethmoidal chamber of *Chimaera*, the ethmoidal grooves on the dorsal surface of the snout of certain of the Selachii also being included in it, as I have suggested in certain earlier works (Allis, 1917, 1926). The cavum praecerebrale forms in early embryos of the Plagiostomi a direct anterior prolongation of the cranial cavity as shown in de Beer's figure of a 45 mm. embryo of *Scyllium* (Fig. 8). This cavum praecerebrale is never lined with dura mater, and in the adult Chlamydoselachus I found (Allis, 1923*b*) the fenestra praecerebralis plugged with tough tissue and the dura mater limited in its forward extension to the hind wall of the plug. There would accordingly seem to be nothing markedly improbable in the assumption that the ethmoidal chamber of *Chimaera* was primarily directly continuous with the actual postorbital portion of the cranial cavity. The cavum praecerebrale, if it actually forms part of the ethmoidal chamber, has, like the orbits, shifted upward to a certain extent after the general cranial flexure had ceased to be reduced, and hence does not in the adult form an anterior prolongation of the forebrain cavity. The presence in the Holocephali of a septum nasi of the selachian type suggests that they are more closely related to the Carchariidae and Scylliidae than to the Notidanidae and Spinacidae, and this further suggests that the frontal knob of the Holocephali may be in some way related to the three-limbed rostral basket of the Carchariidae and Scylliidae.

CYCLOSTOMATA

In *Petromyzon* and hence probably in all of these fishes fertilization is external and the egg is enclosed in a thin and closely fitting membrane.

In a median sagittal section of a 5-day-old embryo of Petromyzon planeri, v. Kupffer (1894) shows the anterior end of the head projecting slightly dorso-anteriorly above the outer surface of the egg, as shown in the accompanying Fig. 14. The headfold is a large angular depression, the bottom of which projects posteriorly ventral to the preoral gut and slightly dorsal to it there is a triangular thickening of the ectoderm apparently wholly due to a lengthening of the related cells. It is called by v. Kupffer the hypophysis, lies approximately external to the recessus preopticus, is directed posteriorly dorsal to the preoral gut and hence apparently lies between cranial and visceral

ectodermal surfaces approximately in the position of the external opening of Rathke's pocket in the Plagiostomi. It is later prolonged posteriorly to the hind end of the infundibulum, a central cavity develops in it and it then has to the infundibulum and the preoral gut the topographical relations of Rathke's pocket in the Plagiostomi. It is therefore quite certainly the homologue of the latter pocket, for that the hypophysis was developed twice independently in the vertebrate line seems improbable. The probable explanation of its markedly different manner of development in this fish and in the Plagiostomi must then be that as the closely fitting egg membrane prevents the anterior end of the head from swinging downward, backward and upward to form a hypophysial fold, that fold is formed by what may be called the gradual and progressive pinching together on the internal surface of the head-fold of two ectodermal surfaces, one cranial and the other visceral, that correspond to the two walls of the hypophysial fold of the Plagiostomi, this pinching off process continuing until the tip of the fold or pleat so-formed reaches the hind end of the infundibulum and becomes the tip of Rathke's pocket.

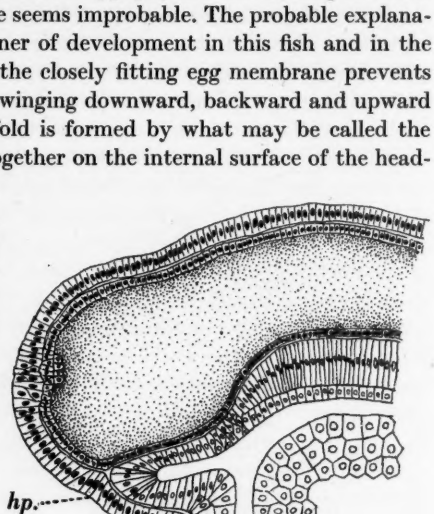

Fig. 14. Median view of the bisected head of a 5-day-old embryo of *Petromyzon planeri*. After v. Kupffer. Reversed in direction.

Anterior to this hypophysis, between it and the median olfactory pit, maxillary processes must develop in later stages as they do in the Plagiostomi, but they have never been described so far as I can find. The buccopharyngeal upper lip then grows forward ventral to these processes and the short pre-hypophysial (intermaxillary) canal so formed is prolonged anteriorly to the end of the snout by the combined growth forward of the maxillary processes and the buccopharyngeal upper lip, as suggested in one of my earlier works (Allis, 1931*a*). This carries the olfactory pit forward to its ultimate position on the dorsal surface of the anterior end of the snout and as the buccopharyngeal upper lip grows forward slightly beyond the maxillary processes, the pre-hypophysial canal opens on the dorsal surface of the snout immediately anterior to the olfactory pit. The snout is thus now definitely of the viscero-trabeculo-cranial type and the conditions in this fish show a slight advance in this respect over those in the Plagiostomi.

The conditions in *Bdellostoma* have been described by v. Kupffer (1900), but he did not have a complete set of embryos, and the conditions described by him differ so markedly in certain respects from those in *Petromyzon* that

any attempt to establish their definite homologies should await further investigation. It may, however, be stated that the prehypophysial canal lies in large part anterior to the single median nasal capsule instead of posterior to it, and that it is enclosed in longitudinal laminar processes, one on each side of the head, that are said to grow downward from the ventral surface of the prenasal portion of the snout. These processes would therefore seem to be maxillary processes similar to those in the Plagiostomi, and the cartilages that develop in them must be of premandibular origin and the cartilaginous rings that enclose the nasal tube of the adult would suggest origin from premandibular branchial rays. The extent to which the buccopharyngeal upper lip extends forward cannot be determined from the descriptions, but it certainly does not extend beyond the tip of the snout. The nasal aperture accordingly opens morphologically on the ventral surface of the snout, as the nasal apertures do in the Elasmobranchii.

GANOIDEI

Little is definitely known about the early development of the prechordal portion of the head of these fishes, but so far as can be judged from existing descriptions the manner of its development differs markedly in certain respects from that in either the Cyclostomata or the Elasmobranchii. It has been most fully and completely described in *Acipenser*, and as the manner of its development is probably, in principle, the same in all of these fishes, that in *Acipenser* alone will here be particularly considered.

In 1893 v. Kupffer gave a figure showing a median vertical section through the head of a 45-hr.-old embryo of *Acipenser sturio*, and, although this figure is probably incorrect in certain details, it presents conditions that can readily be compared with those in *Petromyzon* and is accordingly reproduced in the accompanying Fig. 15. The embryo is said to lie flat on the dorsal surface of the egg with its anterior end curving somewhat anteroventrally. The stomodaeum, which forms the expanded anterior end of the headfold, is a large angular depression near the anterior end of the embryo, between the anterior end of the head and that part of the body that encloses the heart. It is called

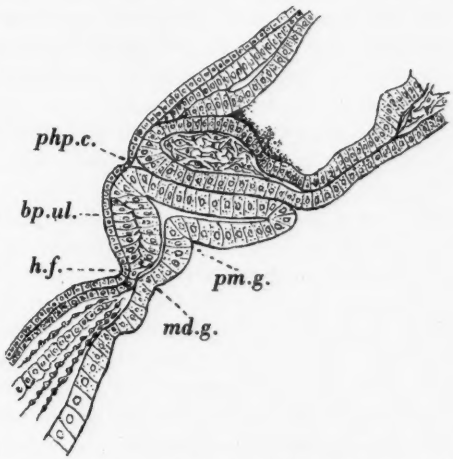

Fig. 15. Median view of the bisected head of a 45-hr.-old embryo of *Acipenser sturio*. After v. Kupffer. Reversed in direction.

by v. Kupffer the "Mund" and its inner end is in contact with the wall of a diverticulum of the gut which he calls the "Vorderdarm", and as this contact persists in all of the older embryos described by him, it evidently represents the buccopharyngeal plate and is so designated by Neumayer (1932) in his descriptions of an embryo of this same age. This diverticulum of the gut, as described by Neumayer, has bulging lateral walls and as these walls apparently become closely pressed together in older embryos the point of the diverticulum and the tip of the stomodaeum, as shown in v. Kupffer's figures, become for a time somewhat widely separated from each other.

The dorso-posterior wall of the stomodaeum forms the ventro-anterior wall of a mass of tissue roughly triangular in median sagittal section that is called by v. Kupffer the adhesive organ and which I have homologized in an earlier work (Allis, 1932*a*) with the buccopharyngeal upper lip of *Petromyzon* and the Plagiostomi. The ventro-anterior and dorsal walls of this lip are of ectoderm, the ventro-posterior one being of endoderm and forming part of the outer wall of the gut. The hollow of the lip is said by both v. Kupffer and Neumayer to be filled with ectoderm, but Sawadsky (1912) and Holmgren (1931) say that it is filled with endoderm, this endoderm being shown in their figures simply as a pronounced thickening of the wall of the related part of the gut. In favour of the hollow of the lip being filled with endoderm instead of ectoderm is Reighard & Phelps's (1908) statement that in *Amia calva* the adhesive apparatus is of endodermal origin. This marked development of endodermal tissue in the buccopharyngeal upper lip of these fishes doubtless accounts for the growth forward, in early embryonic stages, of the lip to the outer surface of the snout.

The median line of the dorsal wall of the buccopharyngeal upper lip forms the ventral half of a strand of cells called by v. Kupffer the hypophysis. This strand is cylindrical in form, with its cells arranged radially about its axis, and it is considered to have primarily enclosed a cavity which has been suppressed by the pressing together of its enclosing walls. This cylindrical strand is quite unquestionably the homologue of the prehypophysial canal of *Petromyzon* and the Plagiostomi and it will accordingly hereinafter be so referred to. The walls of this canal are directly continuous externally with the deeper layer of the ectoderm, a slight sharply pointed depression marking the place where the deeper layer of the ectoderm curves inward to join and become continuous with the walls of the canal. The walls of the inner end of the canal are said by v. Kupffer to be similarly continuous with the endoderm forming the dorsal wall of the gut and are so shown in his figures, but Neumayer says there is here fusion without perforation of the wall of the gut, while Holmgren says that there is contact but no actual fusion, and comparison with *Petromyzon* and the Plagiostomi indicates that this latter conclusion is quite certainly correct.

In slightly older embryos of *Acipenser* than that shown in the figure the inner end of the prehypophysial canal becomes detached from the endoderm,

turns posteriorly beneath the infundibulum and becoming enlarged acquires a central cavity and represents the hypophysis of the adult. This hypophysis is quite unquestionably the homologue of that of *Petromyzon* and hence quite certainly the homologue also of the elasmobranchian Rathke's pocket. The dorsal wall of the prehypophysial canal of *Acipenser* must then correspond to the dorsal wall of the headfold of early embryos of *Petromyzon* and the definitive hypophysis be, morphologically, a fold in that wall, as it is in *Petromyzon* and the Elasmobranchii. Beyond the hypophysis the headfold of *Acipenser* must then turn outward close against its dorsal portion and when it reaches the outer surface of the head turn ventro-anteriorly across the outer surface of the buccopharyngeal upper lip and end in the stomodeal depression.

Internal to the inner end of the prehypophysial canal and hence internal to the anterior end of the definitive hypophysis, there is a small transverse V-shaped groove on the inner surface of the wall of the gut. It is called by Sawadsky the preoral gut and evidently corresponds to Sessel's pocket in the Plagiostomi. That part of the outer wall of the gut that lies between it and the anteroventral edge of the buccopharyngeal plate must accordingly represent the floor of the mandibular section of the alimentary canal which has swung anterodorsally and become considerably elongated in connexion with the marked growth forward of the ventral ends of the mandibular and hyal arches, this all being in some way related to the enclosure of the egg in a relatively close-fitting membranous envelope.

The conditions and the relative positions of the organs here under consideration in early embryos of *Acipenser* are thus markedly similar to those in much older embryos of *Petromyzon*, but the serial order and manner of their development is not the same in the two fishes. In earlier stages of development described by Sawadsky and Holmgren the buccopharyngeal upper lip has already extended forward to the outer surface of the head and is in position for the development of a functional adhesive organ, which, however, never develops in *Acipenser*. There is not the slightest indication of the definitive hypophysis. The headfold begins on the outer surface of the forebrain and extending anteroventrally across the outer surface of the buccopharyngeal upper lip ends in a slightly marked depression which indicates the position of the future stomodaeum. The hypophysis of this fish develops, as shown in the older embryos above considered, in relation to a hypophysial fold in that part of the headfold that covers the ventral surface of the trabeculocranial component of the snout. That component of the snout of these early embryos of *Acipenser* is already completely fused with the dorsoposterior surface of the buccopharyngeal upper lip which forms the visceral component of the snout. In order that a hypophysis may be developed the headfold must accordingly force its way in between these two already fused components of the snout until it reaches the region of the preoptic recess, and this is accomplished by the formation of what Holmgren calls a hypophysial cell plug. This plug is at first simply a marked thickening of the deeper layer of the ectoderm on

the dorsal surface of the snout, the cells of the thickening being at first irregularly arranged. This mass of cells grows inward until its inner end reaches and comes into contact with the dorsal wall of the gut and, according to Sawadsky, it is only after this, at approximately the 45 hr. stage, that the cells assume the columnar shape and a central cavity in the column is to a certain extent indicated. The definitive hypophysis is then developed as a backward growth from the tip of the hypophysial cell plug beneath the infundibulum. The hypophysis of this fish, like that of the Plagiostomi, is thus definitely of ectodermal origin, endodermal cells, if actually present, having become secondarily attached to it.

The snout of *Acipenser* is primarily of the viscero-trabeculo-cranial type, but this cannot be a primitive condition for it is primarily of the trabeculo-cranial type in the Cyclostomata and Elasmobranchii. An adhesive organ apparently only develops on the outer end of the snout when it is of the viscero-trabeculo-cranial type, which would seem to indicate that this organ was not possessed by the ancestors of the Cyclostomata and Plagiostomi. An adhesive organ of this type is evidently needed immediately after the embryo leaves the membranous eggshell, this either accounting for or being the result of the marked early development of the buccopharyngeal upper lip, and as a result of the early development of the latter lip the prehypophysial canal develops before the hypophysis does, this being the reverse of the order of development of these two structures in *Petromyzon* and the Plagiostomi. The prehypophysial canal also here develops progressively from its outer to its inner end, which is the reverse of the manner of its development in *Petromyzon* and the Plagiostomi. The definitive hypophysis, like that of *Petromyzon*, also develops progressively from its outer to its inner end, which is the reverse of its manner of development in the Plagiostomi, and this reversal in the order of development of these structures is evidently due to the necessity of developing a hypophysis under changed conditions imposed by a closely fitting egg membrane.

In *Amia calva* the conditions, as described by Reighard & Mast (1908), Reighard & Phelps (1908) and de Beer (1923, 1926), are apparently strictly comparable with those in *Acipenser*, excepting in that the ventral ends of the mandibular and hyal arches do not grow forward to the level of the tip of the upper jaw at as early an age as they do in *Acipenser*. In Polypterus, which is also one of the Ganoidei, the early development has never been described so far as I can find. Certain authors have however said that the hypophysis of this fish opens on the roof of the buccal cavity, as it does in the Plagiostomi, but I found no indication of this in any of the several specimens that I examined in connexion with an earlier work (Allis, 1922).

CONCLUSIONS

In the Plagiostomi, and probably in all vertebrates, the polar cartilage is the pharyngeal element of the mandibular branchial bar, the trabecular

and palatine cartilages being the dorsal and ventral halves, respectively, of the premandibular branchial bar. The premandibular bars develop in the maxillary processes, the bend at the middle of the length of the curved bar directed anteriorly. The ethmoidal region of the chondrocranium is probably largely if not entirely of premandibular branchial-ray origin.

The so-called septum nasi of the Elasmobranchii, when present, is not a solid median plate of cartilage, always containing primarily a median cavity that represents the ventral portion of an embryonic cavum internasale.

The hypophysis, in the fishes above considered, is developed in relation to what is either actually or in principle a fold or pleat taken in the headfold at a definite place in its length. The tip of the fold or pleat lies approximately opposite the hind end of the infundibulum and approximately between cranial and visceral ectodermal surfaces, the external opening of the fold or pleat lying approximately opposite the preoptic recess. When the embryo, in early stages of development, lies in a body cavity or in a capacious and protective eggshell these two surfaces of the headfold actually swing together and fuse with each other excepting along the median line, but when in early stages of development the embryo is enclosed in a closely fitting and thin egg membrane this swinging together of these two parts of the headfold is replaced by a process of infolding which brings the two corresponding surfaces gradually and progressively in contact with each other internal instead of external to the line of the headfold. The actual swinging together of the two surfaces, which takes place in the Elasmobranchii and probably in all higher vertebrates, is probably always associated with internal fertilization, while the infolding which takes place in the Cyclostomata and Ganoidei is probably always associated with external fertilization.

The conditions in the Teleostei, Dipnoi and Amphibia will be considered in a later work.

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EXPLANATION OF LETTERING

a.c. Alimentary canal.
bp.o. Buccopharyngeal opening.
bp.ul. Buccopharyngeal upper lip.
b.tr. Basitrabecula (Parker).
c.p. Cephalic plate.
emd. Epimandibula.
eth.c. Ethmoidal chamber.
fb. Forebrain.
fb.c. Forebrain cavity.
fnc. Front wall of nasal capsule (de Beer).
fo. Foramen for optic nerve (de Beer).
fol. Olfactory foramen (de Beer).
ft. Foramen for trochlear nerve (de Beer).
h.f. Headfold.
hp. Hypophysis.
ifd. Infundibulum.
lnc. Side wall of nasal capsule (de Beer).
m. Schlussmembran der Präfrontallücke (Gegenbaur).
md.a. Mandibular arch.
md.b. Mandibular bar.
md.g. Mandibular gut.
mnc. Median wall of nasal capsule (de Beer).
mx.pr. Maxillary process.
N. Naselkapsel (Gegenbaur).
n. Notochord.
nc. Nasal cartilage (de Beer).
nco. Outer process of nasal cartilage (de Beer).
n.g. Neural groove.
non. Notch for optic nerve (de Beer).
np. Neuropore.
O. Optic foramen (Gegenbaur).
oc. Orbital cartilage (de Beer).
ol. Olfactorius Bucht der Schädelhöle (Gegenbaur).
ol.p. Olfactory plate.
op.v. Optic vesicle.
or. Orbit.
p.c. Polar cartilage.
php.c. Prehypophysial canal.
pl. Planum antorbitale (de Beer).
pm.b. Premandibular bar.
pm.f. Premandibular section of brain floor.
pm.g. Premandibular gut.
pm.m. Premandibular mesoderm.
p.p. Palatine process.
pr.r. Preoptic root of the orbital cartilage (de Beer).
ps. Praesphenoidvorsprung (Gegenbaur).
R. Rostrum (Gegenbaur).
R'. Medialer Schenkel (Gegenbaur).
r. Lateraler Schenkel (Gegenbaur).
ros. Rostrum.
r.p. Rathke's pocket.
sl. Lateral rostral process (de Beer).
sm. Median rostral process (de Beer).
s.n. Septum nasi.
srp. Suprarostral process (de Beer).
t. Trabecula (de Beer).
tp. Trabecular plate (de Beer).
tr. Trabecula.
tr.f. Trabecular fenestra (Parker).
V. Mediane Leiste des Internasalknorpels (Gegenbaur).
X. Probable tip of Rathke's pocket.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

May and June 1938

RECORDED BY

A. J. E. CAVE

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

MAY 1938

An Ordinary Meeting of the Society was held in the Department of Anatomy, Middlesex Hospital Medical School, at 3 p.m. on Friday, 6 May 1938, with Professor A. B. APPLETON (Vice-President) in the Chair.

Dr R. WHEELER HAINES read a paper on "A revision of the extensor muscles of the forearm in tetrapods."

From an examination of examples of all living orders of reptiles and amphibians with limbs, and of primitive mammals, it is possible to define precisely the musculature of early tetrapods, with the nerve supplies and the courses of the nerve trunks, and to reconstruct these in fossil animals (*Ophiacodon*, *Eryops*). The musculature consists of a radial group, the tractor radii and the extensores radiales superficialis to the carpus and profundus and intermedius to the radius, a humerodorsalis to the metacarpals, an extensorius ulnaris to the ulna and pisiform, and in the forearm and hand, a supinator manus, extensorii digitum breves and dorsometacarpales. The tractor radii is supplied by a special nerve, the other muscles by the n. extensorius cranialis and caudalis (dorsal interosseous and n. to anconeus of man), and the n. extensorius communicans from the flexor region of the forearm.

The living turtles retain the primitive gait, musculature and innervation, and *Sphenodon* still has the four extensor nerves. In urodeles, anurans, lacertilians and crocodiles the muscles and nerves are more specialized. In mammals, with the loss of elevation and depression of the elbow joint and the development of pronation and supination, the muscles have changed. The tractor has been lost, the intermedius has become a flexor, the brachioradialis and the profundus the supinator. The humerodorsalis has extended secondarily to the digits, forming the extensor communis. The extensor ulnaris has formed the anconeus, the extensorius carpi ulnaris and the extensorius digitum ulnaris (V and IV). The n. extensorius caudalis still supplies the anconeus, but both the nerve to the tractor radii and the communicating nerve have been lost.

The nerve supplies of all the muscles except the radial group are variable, but save in anurans the paths of the nerve trunks are constant.

Professor WOOD JONES considered the root nerve supply of greater significance than the nomenclature and topography of peripheral nerves, and disagreed with the account given of the evolutionary history of the crocodilian forelimb.

Dr W. L. STRAUS had independently confirmed the stated primitive insertion of the humerodorsalis muscle. He agreed that the m. extensor digiti quinti proprius was derived from the ulnar extensor mass. He regarded the amphibian muscle pattern as more important than the reptilian, from the phylogenetic viewpoint, and held the connexion described between the flexor and extensor peripheral forelimb nerves to be not a primitive, but a specialized feature.

Professor APPLETON commented upon the parallel changes effected in muscle groups by different methods and upon the constant association between

peripheral nerve trunks and particular muscle masses. He considered the nomenclature of peripheral nerves to be expedient and justifiable and their relationship to individual muscles or muscle groups to constitute valid criteria for morphological argument.

Dr HAINES, replying, welcomes Dr STRAUS's confirmatory evidence of extensor muscle derivation. As an example of the irreversibility of evolution he detailed the phylogeny of the crocodilian forelimb: the elbow joint of the primitive reptile was of approximately condyloid (not enarthrodial) type, and the elbow enarthrosis of the natatorial *Ornithorhynchus* was purely a specialization. Concerning the role of nerve-supply in the determination of muscle homologies, nerves usually afforded very good evidence, but not, however, in the forearm region. The fundamental question had still to be settled—whether or not a given muscle can change the root value of its innervation: Eisler had noted that, in different specimens of monotremes, the same muscle could be innervated through a different series of spinal roots.

Mr K. C. RICHARDSON and Dr F. G. YOUNG read a paper on "Histological observations on the pancreatic islets of dogs made diabetic by injection of crude anterior pituitary extracts".

Houssay and his colleagues have shown that removal of the pituitary gland greatly relieves the symptoms of diabetes induced by pancreatectomy and that intact animals can be made temporarily diabetic by the daily injection of crude anterior pituitary extracts (see Houssay, 1936). Young (1937, 1938) has further shown that, if a large dose of a crude anterior pituitary extract is administered daily to dogs, the diabetic condition may continue after the daily injections cease, and apparently becomes permanent.

The pancreatic islets have been examined in six dogs which had received daily injections of a diabetogenic extract of ox anterior pituitary gland. There appear to be three types of response of the islet cells to these injections:

(*a*) Disappearance of the specific cytoplasmic granules in some of the beta cells in the majority of the islets.

(*b*) Hydropic degeneration in a few beta cells.

(*c*) Proliferation.

Hyalinization of the islets was found in one of the permanently diabetic dogs.

In comparing the changes in the islet cells of these dogs with those found in experimental diabetes following partial pancreatectomy, and in human diabetes, the following points are of interest. Hydropic degeneration, the characteristic lesion in experimental diabetes following partial pancreatectomy with suitable dietary measures (Allen), is not a prominent feature in the intact dogs made diabetic by anterior pituitary injections, and is found only rarely in human diabetes. It has been claimed that a certain proportion of cases of human diabetes show apparently no change at all in the islet tissue. The cytological findings in one permanently diabetic dog in this series probably have an important bearing on this problem. Evidence of the existence of a "pancreotropic substance", acting antagonistically to the diabetogenic factor in crude anterior pituitary extracts, has already been given in rats (Richardson & Young, 1937). The unusual mitotic activity, found in the islets of two dogs during the course of injections of a diabetogenic anterior pituitary extract, may be due to this "pancreotropic substance". An attempt to isolate the "pancreotropic substance" from crude extracts is in progress.

Dr R. G. Inkster read a paper on "Inversion and eversion of the foot and the transverse tarsal joint".

Current British textbooks do not agree in their descriptions of the joint movements which occur during inversion and eversion of the foot. Inaccuracies result from over-emphasis on summation of small movements at the intertarsal joints and from the use of a surgical term, the "transverse tarsal joint".

Numerous small intertarsal movements are important only in that they provide elasticity of the foot when supported by active muscles.

Movement of the calcaneum under the talus is essential to inversion or eversion and fixation of the calcaneum will, for all practical purposes, prevent these movements. It is, therefore, inaccurate to state that inversion or eversion takes place at the "transverse tarsal joint", since the bulk of the movement must take place at the talo-calcaneo-navicular and talo-calcanean joints.

The function of the foot depends largely on its subdivision into three chief portions, and the freely moving joints can be grouped in a similar manner.

(*a*) The talus moves in flexion and extension at the ankle joint.

(*b*) The remaining tarsal bones and the metatarsals are bound together as a comparatively rigid but sufficiently elastic mass which moves under the talus and round its head during inversion and eversion. This part forms the arches of the foot and transmits the weight of the body to the ground. The joints concerned are the talo-calcaneo-navicular and talo-calcanean joints.

(*c*) The remaining more mobile portion lies anterior to the heads of the metatarsals.

The calcaneo-cuboid joint, although one of the joints in the more rigid middle part of the foot, is permissive in relation to the movements of inversion and eversion in that it allows the forepart of the foot to move round a different axis from the axis of movement of the calcaneum.

The term "transverse tarsal joint" is misleading and should be discarded.

Professor Lockhart showed a radiograph confirmatory of the substance of this paper: he adduced clinical evidence in support of its thesis, but pointed out that full inversion implies some adduction at the calcaneo-cuboid junction.

Professor Johnston drew attention to the true value of movements of inversion and eversion in the normal posture, i.e. with the body weight transversing the foot to the ground: in the resting erect posture, the foot was really everted whilst in the active erect posture the foot becomes inverted. The maximal range of tarsal movement occurs between the internal cuneiform and the first metatarsal and this joint is invested with considerable clinical importance.

Dr MacConaill stated that the evidence derived from a study of the foot ligaments indicated that the movements of inversion and eversion really began at the ankle joint; the transverse tarsal joint was surgically, if not anatomically, important: in standing the calcaneum and the astragalar head formed the head of a distinctively human screw mechanism.

Dr G. I. Boyd discussed the terminology of the tarsal joints.

Professor Appelton referred to previous German investigations of foot mechanisms, both on cadavera and on living subjects. A rotation or medial sliding was effected between calcaneum and cuboid: Fick's observations showed that the transverse tarsal joint has genuine functional significance, in permitting dorsoventral movement in the primate foot.

Dr Inkster, in reply, stated that his present paper resulted from personal observation. He agreed that considerable movement occurs between the

internal cuneiform and first metatarsal bones, and recommended the shape and disposition of articular surfaces as reliable evidence of the range of movement possible to individual tarsalia.

Drs S. J. FOLLEY and S. ZUCKERMAN read a paper on the "Development of the mammary gland in the *Rhesus* monkey".

The area of the mammary gland in the female *Rhesus* monkey between the range of body-weight of 2–6 kg. increases relative to the increase in body surface according to the simple allometric growth law. Duct development in the female monkey shows itself before external signs of puberty are observed and before menstrual cycles are established. The duct system continues developing during the first menstrual cycles, but alveoli do not become apparent until luteinization has occurred. The mammary gland in the normal male *Rhesus* is rudimentary, but the duct system can be experimentally developed by means of the injection of oestrone. Such treatment did not cause alveolar formation even after a period of a year's daily injections. Contrary to observations that have been made on mice, neoplastic changes have not been observed in the mammary glands of male and female monkeys that have been injected for periods of from one to two years with relatively large amounts of oestrone. Testosterone proportionate apparently stimulates alveolar formation along with stunted development of the ducts.

Professor WOOLLARD discussed the mathematical notation of allometric growth. He asked whether the large amounts of oestrone injected affected tissues other than the mammary, and whether the effects of male and female hormones are an expression of similarity of chemical structure.

Dr ZUCKERMAN, replying, stated that the earliest menstrual cycles were unaccompanied by ovulation. Hormones are confined in action to specific tissues and though chemical structural similarity exists between male and female hormones, this disappears in biological study of hormonal action, the effects of either male or female hormone being distinguishable microscopically.

Mr E. W. PEET spoke on "The anatomy of the internal ear". He illustrated the relative positions of the semicircular canals in European skulls of different cephalic index, described his method of wax plate reconstruction of the internal ear and his technique for making preparations of the membranous labyrinth. This last is as follows:

The temporal bone is cut down to as small a size as possible without opening into the labyrinth. The stapes is then removed to allow entry of fixing fluid and other substances into the labyrinth. After fixation and thorough dehydration, the bone is immersed in a solution of 2% celloidin. This is hardened by the chloroform vapour method. The bone is now immersed in 56° melting point paraffin wax which enters the labyrinth cavity and mixes with the celloidin already there. After cooling, the exterior of the bone is scraped free of wax and decalcified in 50% HCl. After decalcification and washing a cast of the labyrinth cavity is left free which is composed of a mixture of paraffin wax and hardened celloidin. Inside of this is the membranous labyrinth. The cast is placed in celloidin solution which is hardened by chloroform vapour. After hardening the block of celloidin is placed in xylol which penetrates through it and dissolves the wax from the cast. The block is finally cleared and mounted in benzene.

Professor WOOLLARD enquired whether it was practicable to inject the labyrinth with a radio-opaque substance.

Dr MACCONAILL recommended the employment of wax-impregnated typewriting paper for reconstruction work, as being both unshrinkable and unbreakable.

Professor APPLETON commented upon the elegance of the labyrinth preparations: he recommended the adoption of a standard cranial orientation in further investigations of the relative positions of the semicircular canals.

Mr PEET replied, acknowledging the remarks made.

DEMONSTRATIONS

At this Meeting of the Society the following Demonstrations were given:

(1) F. P. REAGAN: Illustrations of the veins draining the gill regions of embryos.

(2) C. F. V. SMOUT: Dissections of comparative anatomy, viz.: (*a*) the spleen in racing and non-racing breeds of the same species, (*b*) mammalian uteri of different types, (*c*) equine testis showing the well-developed cremaster muscle.

(3) E. W. PEET: (*a*) Reconstructions of the human internal ear, (*b*) specimens of human membranous labyrinth, (*c*) series of micro-preparations of mammalian labyrinths fixed *intra vitam* and subsequently stained by various methods, (*d*) an age series of human skulls dissected to show the relative positions of the semicircular canals of the two sides.

JUNE 1938

The Summer Meeting of the Society was held at the Royal College of Surgeons of England, at 9.30 a.m. on Friday and Saturday, 17 and 18 June 1938, the President, Professor ALEXANDER LOW, in the Chair.

Dr G. M. WYBURN read a paper on "The formation of the umbilical cord and the umbilical region of the anterior abdominal wall".

The umbilical cord, first established in embryos from about 5–7 mm., is formed by the growth of lateral tissue plates of junctional mesoderm extending from the allantoic stalk to the septum transversum.

The umbilical cord coelom enlarges by the extension of its endothelial lining into large spaces in the cord tissue, and following the ventralization of the gut is obliterated by the proliferation of dense fibrous tissue which forms an encircling collar at the embryonic attachment of the cord.

This circular zone of mesodermal condensation also contributes to the abdominal parietes and reinforces the linea alba above and below and the rectus sheath on each side.

Some fault of the junctional mesoderm, i.e. the tissue of the embryonic rim where there is union of primary and secondary mesoderm, is responsible for congenital herniation which results either from maldevelopment of the cord itself or from defects of adjacent parietes.

Professor BLAIR emphasized the importance of the "junctional mesoderm" and alluded to the instability of the umbilical area of the anterior abdominal

wall: the developmental account given in this paper provided an explanation of the congenital abnormalities encountered in the umbilical region. Professor J. P. HILL accepted the suggestion that the umbilical coelom disappeared by the proliferation of surrounding mesoderm.

Dr F. P. REAGAN read a paper on "Variant dorsal parietal veins described in 1891 by Professor Arthur Robinson".

In studies from Owens College, Robinson gave us these concepts: that embryonic renal veins cannot possibly be intersegmental tributaries to Vv. cardinales posteriores; that if V. hemiazygos persists near the level of V. renalis sinistra it is likely to have transverse anastomosis with the latter; that this anastomosis is the bilateral homologue of a morphologically transverse portion of V. cava at the immediately postrenal level. He noted that early longitudinal dorsal veins are connected at all intersegmental levels by transverse prevertebral anastomoses. Having noted this at the renal level, and having emphasized the two transverse elements above referred to, he gave us an adult basis for the embryonic circulus venosus renalis (renal collar). He showed that where lumbar veins unite into a single stem, such a stem has been derived from the dextral portion of a transverse prevertebral anastomosis. He established negative correlation between these phenomena; the tendency of sinistral longitudinal veins to persist as variants collateral to postrenal V. cava; tendency towards Y-shaped configuration of lumbar veins.

An attempt will be made to apply these concepts to recently observed vessels.

Most of the figures shown will appear in publication jointly with Professor Robinson.

Professor WOOLLARD remarked that veins tend to preserve the primitive embryonic capillary pattern and that the morphological interpretation of particular venous channels must be fraught with extreme difficulty: a given definitive vein stem might arise in a variety of ways.

Dr GLADSTONE spoke of the fundamental importance of Professor ROBINSON's earlier studies of the embryonic vascular system, which appropriately formed the basis of the present paper.

Dr BRANDT referred to Adachi's researches upon the venous system and its variation in the Japanese as illustrating the difficulties inherent in the understanding of particular vascular patterns. A possible factor in the production of inferior caval anomalies was variability of renal form and position.

Dr R. J. O'CONNOR read a paper on "Vital staining experiments on the development of the amphibian pronephric duct".

In *Amblystoma tigrinum* and *Triton taeniatus* the first indication of the nephric system is a collection of cells beneath the ectoderm at the ventro-lateral border of the third to sixth somites. The portion under the third and fourth somites develops into the pronephros while that under the fifth and sixth increases in length in a caudal direction to meet the cloaca and become canalized to form the pronephric duct. Being immediately under the ectoderm this caudal extension is visible to external examination. The manner of this extension is not certain, it may either be a growth caudally of the original rudiment or an addition to it by successive segments in a caudal direction.

Localized staining of the developing pronephric duct has been carried out. The overlying ectoderm was dissected back and a small piece of agar impregnated with Nile blue sulphate pressed against the exposed duct. The caudal

extremity of the duct was stained at various stages of development. During the next 48 hours the stain was seen to spread as a streak along the line of the developing duct towards the cloaca, and this spread kept pace with the growth of the duct. Examination of serial sections showed that this extension was due to the presence of the dye in the cells of the pronephric duct.

It appears therefore that at least some of the cells in the caudal portion of the pronephric duct are derived from a caudal growth of the original rudiment formed under the fifth and sixth somites.

Professor J. P. HILL welcomed this experimental investigation into the developing urodele pronephric duct, as establishing definitely that growth of this structure occurred by caudal extension and not by the aggregation of multiple segmental portions, such as characterized the higher vertebrates.

Dr BRANDT commented upon orthotopic and heterotopic transplants of the pronephric primordium and their fate in the light of Dr O'CONNOR's researches: orthotopic transplants grew well in their new environment, but heterotopic transplants fared badly.

Dr W. BRANDT read a paper on "The size of the vomero-nasal organ in a 12·5 mm. human embryo".

Statements in the literature concerning the size of the vomero-nasal organ in human embryos are mostly given in a general way. Most authors mention a very "large" organ in early developmental stages which gradually atrophies in later stages. Some measurements of the length of the vomero-nasal organ in mm. have been made. But the length alone is not the real expression of the degree of development, because the masses of the cells which constitute the wall of this organ are not included in a measurement of the length alone. The thickness of the wall of the vomero-nasal organ is about three times as thick as the mucous membrane of the nasal cavity.

The first results are given of (1) a percentage calculation of the mass of the whole vomero-nasal organ on both sides in relation to the whole mucous membrane of the nasal cavity; (2) a calculation of the quantitative relations of both vomero-nasal organs to that part of the mucous membrane of the nasal cavity which belongs to the same level of development of the organ in the nasal cavity; (3) a calculation of the quantitative relations of both vomero-nasal organs to the mesoderm of the nasal septum, which belongs to the same level of their development. The percentages are the mathematical expression of the degree of the tridimensional development of the vomero-nasal organ. They give at once the quantitative relations to other tissues and an indication of the embryological constitution of any part of the body. Therefore these numbers are more accurate than the terms "large" or "small" or a simple measurement of the length alone, of any organ.

Dr G. BOURNE read a paper on 'Functional changes in the adrenal gland of the Australian opossum".

The adrenal gland of the male opossum has a thin cortex and a voluminous medulla.

Pouch young female opossums have adrenals somewhat similar to those of the male. Young half-grown females have adrenals which show thickening of the cortex on one side of the organ.

In mature females this zone has enlarged to occupy quite a considerable portion of the gland. In young virgin females the zone is composed of small

darkly staining cells (*beta* cells) quite different from the lipoid-containing cells or spongiocytes of the adrenal cortex (*alpha* cells). In mature non-pregnant females the cells in the hypertrophied area are still of the same small dark variety. With the onset of pregnancy there is a metamorphosis of these cells in the inner three-quarters of the gland to large cells with the cytoplasm showing a marked affinity for eosin (*delta* cells). There appear to be about three or four of these cellular cycles during pregnancy and lactation. Neither *beta* nor *delta* cells contain appreciable quantities of fat, which appears to be restricted principally to the *alpha* cells, occupying a thin peripheral ring in the gland. This zone differs from the "X zone" of mice and rats in that it is a zone of sexual maturity, rather than a "juvenile zone".

Mr BURNE enquired concerning the specificity of certain cellular elements described, and was informed that the *beta*-zone cells grew and metamorphosed into *delta* cells.

Dr P. BACSICH and Dr S. J. FOLLEY read a paper on "Effect of high doses of oestradiol monobenzoate on the endocrine glands, gonads and mammae of lactating rats".

Studies, now in progress, on the endocrinology of lactation provided an opportunity of observing the effect of high daily doses (1 mg.) of oestradiol monobenzoate on the endocrine glands, gonads and mammae of intact and ovariectomized lactating rats.

The central feature of the resulting symptom-complex is the enlargement of the anterior lobe of the pituitary—haemorrhagic chromophobe adenoma.

Thyroids were lighter than those of normal controls; the large acini were full of colloid, thus indicating hypofunction.

There was marked hypertrophy of the adrenal cortex, with hyperaemia, cystic and vacuolar degeneration; the medulla appeared unaltered. Inside the zona reticularis a layer of large rounded cells, so far not described in the literature, was distinguished in both normal and experimental rats. Their appearance and staining properties suggest that they belong to the cortex. This layer was somewhat diminished in oestrogen treated rats.

In the ovaries there was a marked luteinization, with large corpora lutea, small miliary ones, and scattered luteal cells. Graafian follicles showed atretic changes.

Mammary glands showed practically no sign of involution, though lactation had been inhibited to such an extent that all the young had died some days before autopsy of the mothers.

The authors explained that the animals used had ceased to lactate as proved by their progeny dying from inanition. Their mammae, on histological examination, did not reveal the changes normally encountered in the involuting gland after weaning; rather microscopic mammary structure remained unaltered despite the loss of mammary function through lack of the pituitary lactogenic hormone.

Dr ZUCKERMAN discussed the large corpora lutea found in the lactating experimental animal: he asked why, if lactation continues in ovariectomized rats, the injection of oestrin should maintain the normal mammary histological picture. He criticized certain terms employed by the authors, notably that of "pituitary adenoma", and discussed the nomenclature used by Zondek and by Kramer and Horning. Professor DAVIES asked the nature of the large eosinophile cells described in the rat's adrenal cortex.

In reply the authors stated that oestrogenic hormone alone suffices for the maintenance of mammary histology and that the effects of ovarian activity throughout the animal's pregnancy should not be forgotten. The pituitary changes observed seemed to be of the nature of a simple tumour—hence the terminology employed. The thyroid and parathyroid changes resulting from such experiments required further study: in the present series a decrease of thyroid weight had been observed, but both increase and decrease of thyroid weight following oestrogenic hormone injection are reported in the literature. The nature of the adrenal cortical eosinophile cells was quite unknown; the adrenal cortex manifests great histological variability in animals of different species and in the same species according to the various phases of physiological activity.

Mr J. F. Robinson (introduced by Professor J. P. Hill) read a paper on "The essentials of Romanowsky staining processes".

The once-popular Jenner stain is often said to have foreshadowed modern staining fluids of the Romanowsky type. This claim can hardly be allowed, since the essence of Romanowsky's discovery was a staining reaction which could not be attributed either to eosin or to methylene blue, the only dyes present in Jenner's stain. In recent years the chemistry of the Romanowsky effect has become more fully appreciated, and MacNeal has shown that satisfactory staining depends upon the presence of dyes other than eosin and methylene blue. The object of this paper is to show that the methods of preparing Romanowsky stains due to Leishman and Wright are not wholly satisfactory, and to describe an alternative method which affords more consistent results.

Dr de Beer welcomed this informative paper which essentially expounded Hasting's modification of Mott's stain, with one notable improvement—the regulation of acidity.

Dr Bacsich argued that most staining processes were empirical rather than strictly scientific in nature; he had found thirteen out of fifteen examples of Sudan III, from different manufacturers, to exhibit most variable staining properties, despite their identity of chemical composition. In repeating any staining technique it was essential to employ dyes from the same source as those used by the author of such technique. Professor J. P. Hill testified to the value of the alternative staining method described in connexion with routine class work and spoke of its advantages in certain clinical laboratory tests. Dr Stewart quoted the work of Kay and Whitehead to the effect that Sudan III's staining properties are really due to the presence of Sudan IV; on the contrary Dr Bacsich had found Sudan IV an extremely disappointing stain. Replying, Mr Robinson described the methods of large-scale manufacture of coal-tar product dyes, indicating how the very nature of such processes precluded any guarantee of chemical identity of composition in consecutive batches of dyes. The repetition of an original staining technique under precisely identical chemical conditions was quite impossible. Some account was given of the mode of preparation of food-stuff dyes and of the chemical constitution and colour purity of the dyes themselves.

Professor T. Nicol gave a résumé of his researches into fat distribution in the guinea-pig female reproductive tract, and described the results obtained from his intra-vitam staining of the ferret uterus.

In guinea-pigs with a regular oestrous cycle fat is found in the uterine and glandular epithelium and in large wandering cells especially abundant in the stratum compactum. The amount and distribution of the fat varies in different animals but in general the maximum deposition occurs in the luteal and early follicular phases of the cycle. In some animals the fat in the epithelium is present throughout the horns and body of the uterus; in others, mostly in the horns; and in others, mostly in the lower part of the body. In a few animals fat may be practically absent, and it is never found in the vagina.

In guinea-pigs pregnant for $11\frac{1}{2}$, $12\frac{1}{2}$ and $14\frac{1}{2}$ days, "fat masses" are found in the decidua around the embryos. Fat is also found in the epithelium of the uterine horns between the embryos as well as in the lower part of the body and in the vagina. In the uterine horns cells laden with fat and apparently migratory, occur. There is evidence that fat accumulates in the decidual cells by the bursting of these "fat carriers". Fat is also present in the yolk-sac endoderm.

In the ferret the most intense vital staining was found in the uterine horns when the vulva was 9 mm. in diameter, i.e. about the middle of the follicular phase. These results are based on 30 animals examined during the resting and follicular phases of the cycle. The amount and intensity of the staining is strikingly less than in the guinea-pig. The vitally stained cells are confined to that part of the endometrium which is adjacent to the mesentery and contain only a moderate amount of dye. Vital staining is apparently absent at full heat and at the resting stage.

Professor J. Beattie exhibited, on his own behalf and that of Mr L. O'Shaughnessy and Dr D. Slome, a coloured ciné film of "Revascularization of the heart" in both human and animal subjects.

The President commented upon this remarkable film and upon the clinical value of the operative surgical innovations it depicted.

Sir Arthur Keith read a paper on "A resurvey of the anatomical problems raised by the human fossil discoveries at Piltdown and Swanscombe".

After allowing the problems relating to the anatomical characters of Piltdown man to lie at rest for twenty-four years the author of this paper has been moved to make a resurvey of the question because of the following circumstances: (1) the discovery of part of a human skull in mid-Pleistocene deposits by Mr A. T. Marston in 1935–6, (2) the publication of various adequately documented reconstructions of the Piltdown skull, (3) the light thrown on these problems by the recent discovery of early human fossil remains in China, Java and Africa, (4) the experience gained in assisting Mr Theodore McCown to investigate and describe the fossil human remains from Mount Carmel, Palestine, (5) the accumulation of evidence favouring the opinion that similar structural changes may occur in separated branches of the human stock. The chief conclusions reached are the following: (1) The Piltdown brain was asymmetrical to an extent not known in any other race, the association areas of the left hemisphere greatly exceeding in extent those of the right. These features are reversed in Swanscombe man, and are of lesser degree. (2) That in the Piltdown skull itself there are not only characters which may be described as modern—or ultra-modern—but also others—both in the skull and the endocranial cast—which are more primitive or simian than those seen in any other fossil skull. (3) That the Piltdown skull differs in its characterization

from the early fossil skulls of Western Asia to an extent which compels the presumption that there were contrasted types of early Pleistocene man—viz. the Eastern or Oriental type (represented by the discoveries made in China and Java), and a Western or Occidental type (represented by Piltdown man). Using Drennan's terms the Oriental type may be described as "gerontomorphic" and the Occidental as "pedomorphic". So far as they are known, the early African types differ from these two types by sharing in the characters of each. (4) The Piltdown endocranium here exhibited, together with the reconstruction of the skull, displaces 1270 c.c. of water: in the author's 1914 reconstruction the cranial capacity was estimated at 1400 c.c.

Professor LE GROS CLARK commented upon the value of the cranial and endocranial reconstruction. He regarded the Piltdown skull as essentially modern in type and questioned whether many of its so-called primitive features might not be encountered in any sufficiently wide range of definitely modern crania. Professor WOOD JONES welcomed the final settlement of the vexed question of the midline of the Piltdown cranium: no human skull was ever truly symmetrical.

Sir ARTHUR KEITH, replying, explained more fully his particular employment of the term "modern" in connexion with this human fossil, and his changed personal views concerning its modernity. Piltdown man, in his cranial anatomy, was not truly modern, but pseudomodern, i.e. he foreshadowed closely the cranial form ultimately assumed by modern man. He did not doubt the validity of the association of the mandible with the skull.

Sir ARTHUR KEITH read a further paper on "The Florisbad skull and its place in the sequence of South African human fossil remains".

The Florisbad skull was discovered in 1932 by Professor T. F. Dreyer at a depth of 20 ft. in a stratified deposit at Florisbad in the Orange Free State, 25 miles north of Bloemfontein. The cultural objects which accompanied the skull have led Professor Dreyer to assign it to a date in the "middle stone age" of South Africa—a date which would make Florisbad man contemporary with Neanderthal man in Europe. It is thus the earliest of South African human fossils found under circumstances which permit assessment of its geological age. The skull has been reconstructed and described by Professor Dreyer (*Proc. Acad. Sci. Amst.* 1935, vol. XXXVII, pp. 119–28); its endocranial cast has been described by Dr Ariens Kappers (*Proc. Acad. Sci. Amst.* vol. XXXVII, pp. 119–28) and by Dr A. J. D. Meiring (*S. Afr. J. Sci.* 1937, vol. XXXIII, p. 960). Professor Raymond Dart presented a cast of the Florisbad skull to the Museum of the Royal College of Surgeons which, so far as known, is the first copy to reach Europe. In its frontal characters the Florisbad skull recalls that of Rhodesian man, the supraorbital width being 136 mm. and the minimal frontal width 120 mm. The vertex of the skull, so far as it is preserved, resembles that of the Boskop skull. The malar bones and the facial part of the superior maxilla are modelled as in the Bushman. Its characters are best explained by regarding it as a transitional form leading from the older Rhodesian type to the later Boskop type. This is also the opinion which is held by most of the South African anatomists and is explicitly enunciated by Dr Alexander Galloway (*Amer. J. Phys. Anthrop.* 1937, vol. XXIII, p. 1; *S. Afr. J. Sci.* 1937, vol. XXXIV, p. 89), who detects in it resemblances to the Wadjak type of Java.

Professor WOOD JONES noted the faulty alignment of the malar bone in

the Florisbad reconstruction and suggested its correction in future casts. Dr GALLOWAY agreed that Florisbad man ranked in status as *Homo sapiens*; a comparison of the Florisbad specimen with the Boskop skull and with Australian aboriginal skulls revealed the extensive occurrence of Florisbad features in these latter types, an association indicating the strong probability of racial affinity between the Florisbad and Wadjak men. The Florisbad skull materially facilitated the solution of fundamental problems affecting the physical anthropology of South Africa. It not only satisfactorily linked the Rhodesian and later Boskop forms but also provided an indigenous ancestral origin for, and an explanation of, those so-called "Australoid" features so commonly obtrusive in South African cranial material. The term "Australoid" employed so far in this connexion for want of a more satisfactory designation could now be advantageously discarded.

Dr A. J. E. CAVE read a paper on "The morphological constitution of the odontoid process".

The odontoid comprises two distinct vertebral centra: (1) the larger basal odontoid, (2) the smaller apical odontoid element (co-called apical epiphysis): both are pierced by the notochord (Gladstone (1915) in *Homo*, Barge (1917) in *Ovis*, Hayek (1923) and Dawes (1930) in *Mus*) and both are mutually related to the first hypochordal element, with which they permanently articulate. The apical odontoid is none other than the "pro-atlas", a vertebral centrum fusing with the occipital in reptiles but with the atlantal centrum (=basal odontoid) in mammals. This apical (proatlantal) centrum possesses a degenerate neural arch and its own spinal segmental nerve (the suboccipital). Its neural arch is represented by that portion of the atlantal neural arch lying cranial to the plane of exit of the first spinal nerve; its embryology has been described by Barge (1917–18) and Dawes (1930). The acceptance of the true centrum nature of the apical odontoid establishes the correct alignment of spinal nerves relative to vertebrae, i.e. the suboccipital is related to the apical centrum, the second cervical to the basal odontoid and the third cervical to the centrum proper of the axis, an arrangement harmonizing with vertebro-spinal sequence throughout the remainder of the axial skeleton.

Morphologically, therefore, the atlanto-axial complex comprises, not two, but three successive vertebral elements.

Sir ARTHUR KEITH approved the interpretation of vertebral parts suggested.

Dr DE BEER emphasized the importance of a correct conception of the anatomy of the cranio-vertebral junction, the embryology of which, in the various classes of vertebrates, he detailed in support of the arguments submitted in this paper.

Professor C. M. WEST demonstrated a "Mediaeval achondroplasic skull".

During road excavations in the village of Mounton, near Chepstow, a mediaeval graveyard was opened up, and among the bones discovered was the present specimen, reported to the anatomist as a female brachycephalic skull. Later direct examination of the actual specimen, however, revealed the basal contraction and vault expansion so characteristic of achondroplasic crania, as well as certain other suggestive features. The rest of the skeleton was not available: the skull is demonstrated because of the rarity of achondroplasic specimens.

Professor BRASH regarded the specimen as definitely achondroplasic from

the peculiar configuration of its basi-cranial component, particularly in the occipital region. Dr CAVE said the skull closely resembled certain known achondroplasic crania in the Royal College of Surgeons Museum, which were exhibited for comparison with the present specimen.

Dr J. H. GRAY read a paper on "Experiments on lymphatic regeneration".

Attempts were made to determine the regenerative capacity of lymphatic trunks and capillaries in the rabbit. First, isolated lymphatic trunks possessing uninterrupted course were obtained by constructing tubed pedicles in the skin of the flank. The number, position, and size of these lymphatic trunks in the pedicles were estimated by radiographs taken after thorotrast injection, and the normal state of lymph flow in them noted from the duration of their X-ray shadow. The pedicles were then divided transversely, a small portion containing the whole thickness of the pedicle was removed for histological examination, and the cut surfaces of the shortened pedicle were then resutured end-to-end. The fate of the severed trunks was then watched by subsequent thorotrast injection. Modifications of these experiments were tried in which a cut end of one pedicle was implanted into the ordinary skin of the flank, and secondly one in which a cut end was sutured to a freshly incised free end of a previously constructed pedicle stump.

The findings to date indicate that the cut ends of the lymphatic trunks become sealed off, but there is no extensive thrombosis of these vessels. The lymphatics may thus contrast with the small blood vessels. The lymphatic trunks on the peripheral side of the incision become considerably dilated, and their contents stagnate within the lumen. At 8 days there was neither sprouting of the lymphatic trunks nor lymphatic capillary anastomosis. In 3 weeks, while there was still no macroscopic sprouting of the sealed off lymphatic trunks, there was capillary anastomosis across the line of incision from some of these trunks to those on the central side. In a specimen killed at 26 days there were signs of capillary lymphatic growth while the lymphatic trunks showed no gross changes.

Professor WOOLLARD congratulated the author upon his fashioning of a technique suitable for the investigation of various problems connected with the physiology and pathology of lymphatics. In the regeneration of lymphatic vessels apparently nothing more than a mere capillary anastomosis can be expected. He was informed that in those lymphatic capillaries which united across the suture line no valves had been detected, and that previous workers had likewise failed to observe any such valve formation. Professor DAVIES enquired concerning the mode of lymphatic regeneration as compared with regeneration of blood vessels. Dr GRAY replied, saying that blood vessel capillaries regenerated quickly (in 2–4 days) but lymphatic capillaries more slowly (in about 8 days); new blood vessels can be rapidly and easily formed from the general capillary network. These lymphatic sprouts are of the nature of highly specific endothelial growths, at first solid, but later becoming canalized. Mr WHILLIS asked to what extent regenerating lymphatic capillaries can be influenced by increasing the lymph volume to be drained through them. Dr GRAY replied, with the slow rate of lymphatic regeneration there was a period of marked lymphatic oedema; whether obstruction of neighbouring lymphatics would result in the formation of larger vessels in the pedicle owing to greater lymph flow through them would be investigated later.

Professor F. Wood Jones read a paper on "Air sinuses of the face in the gorilla".

On opening the so-called maxillary sinus of the gorilla the anterior part of the cavity is seen to be occupied by the enormously dilated lower end of the naso-lachrymal duct (bulla ossea nasolacrimalis), the inferior orifice of which enters the inferior nasal meatus in the usual manner. The remainder of the maxillary cavity communicates with the nasal fossa (middle meatus) through an aperture situated behind and above the maxillo-palatine suture, i.e. actually in the ethmoid bone itself. The evidence of immature gorilla skulls indicates that this so-called maxillary sinus is essentially an ethmoidal diverticulum (i.e. a posterior ethmoidal antrum), which secondarily invades and occupies the body of the maxilla.

Professor Le Gros Clark remarked that the opening was not in the position actually of a "posterior" ethmoidal sinus. Dr Cave enquired concerning the possible function of the naso-lachrymal dilatation. Professor Wood Jones, in reply, emphasized the origin of the antrum as an ethmoidal, not a maxillary, diverticulum; the antrum was not primarily maxillary and should not therefore be termed such.

Professor W. E. Le Gros Clark read a paper on "The cortical connexions of the centre-median nucleus".

Dr S. Sunderland read a paper on "The production of cortical lesions by devascularization of cortical areas".

An investigation into the blood supply of the cerebral cortex and the production of cortical lesions by interference with that supply indicates that the cerebral cortex receives its entire effective supply from superficial pial vessels. Any supply by ascending vessels from the subjacent medulla is functionally insignificant. The extent to which the subjacent medulla is supplied from superficial cortical vessels varies.

In small lesions involving narrow, well-folded convolutions, the medullary damage is a minimum and almost certainly involves only the fibres arising in the devascularized area. In larger lesions involving larger, less convoluted areas, the medullary damage extends more deeply. In such cases, although the line of degeneration suggests that the changes involve only the territory conveying fibres arising in the devascularized area, involvement of fibres of passage cannot be definitely excluded.

Professor Le Gros Clark remarked upon the great value of the author's technique particularly with regard to the making of precisely corresponding lesions in different animals or in different parts of the same brain. Dr Sunderland had demonstrated the functional insignificance of the arteries ascending to the deeper cortical layers. Dr Gray asked if it had been possible to confirm the existence of the cerebral arterio-venous anastomoses which Pfeiffer said were present. Dr Sunderland replied that though he had not seen them he did not doubt their existence.

Dr G. A. G. Mitchell read a paper on "The nerve supply of the gastro-oesophageal junction".

The gastro-oesophageal junction receives a nerve supply from supra- and infra-diaphragmatic sources, and from both sympathetic and para-sympathetic elements of the autonomic nervous system. The supra-diaphragmatic sympathetic supply for the *lower* oesophagus is derived partly from the thoracic

portions of the gangliated sympathetic trunks and partly from the splanchnic nerves. These oesophageal filaments are small, vary in number, and often supply twigs to the descending thoracic aorta. Sometimes one filament arising from the region of the sixth or seventh thoracic ganglia is larger than the others, and in several cases a delicate nerve was discovered lying postero-lateral to the descending aorta and linking together the cardiac, pulmonary, aortic and oesophageal filaments of the gangliated trunks and splanchnic nerves; this *para-aortic* nerve terminated above the diaphragm by supplying the lower ends of the oesophagus and thoracic aorta.

The gastro-oesophageal junction receives sympathetic filaments from several infra-diaphragmatic sources, but mainly from the coeliac plexus. Occasionally it receives twigs directly from the termination of the left greater splanchnic nerve or from the upper end of the left lumbar gangliated chain. From the coeliac plexus nerves are conveyed to the junction along the left gastric, left inferior phrenic and sometimes along the right inferior phrenic plexuses, and it also receives a twig from the hepatic plexus which passes across high up between the layers of the lesser omentum, close to the hepatic branch of the anterior vagal trunk.

Professor BLAIR, discussing phrenico-coeliac communications, said that such arrangements did not affect true phrenic action. He suggested a microscopic examination for ganglia of the para-aortic nerve, the exact morphology of which varied much in different animal species. Dr BRANDT had noted in the foetus a constant branch from the coeliac plexus to the cardiac end of the stomach. Professor DAVIES enquired as to the present state of experimental work upon the innervation of the gastro-oesophageal junction. Dr MITCHELL replied, stressing the extremely risky nature of operative interference (by neurotomy or vessel denervation) with the cardio-oesophageal mechanism because of its multiple innervation: denervation of the left gastric artery, to relieve achalasia, had proved but partially successful.

Drs J. DIXON BOYD and J. S. BAXTER read a paper on "The neural crest in a 10-somite human embryo".

This embryo shows a well-developed crista neuralis rostralis on the right side which is not subdivided into an optic and a trigeminal portion. On the left side the crista neuralis rostralis is present, but much less obvious. The primordium acustico-facialis is peculiar in that it is represented by a large mass of neural crest material in the mid-line dorsal to the neural tube which is closed at this level. This mass shows no sign of division into right and left portions. Caudal to this mid-line acustico-facial neural crest primordium there is a bilateral crista neuralis post-otica which is more or less continuous in the somite region with a poorly developed crista neuralis spinalis. There is no definite evidence concerning the mode of origin of the neural crest material in this embryo, but certain sections suggest that it arises from the neural tube. The subdivisions of the neural crest in this embryo and in other human embryos of about the same stage of development are discussed.

Professor J. P. HILL discussed this communication, illustrating his remarks by lantern slides of embryos from his own collection, showing para-medullary masses of proliferating ectoderm. He believed the acustico-facial ganglia to arise from the otic vesicle. Professor LE GROS CLARK enquired as to the nature of the asymmetry in this embryo and was informed that the tissues of the right side predominated. Dr BOYD summarized the authors' opinions

of mammalian neural crest cells based upon their present specimen and two of similar age of Professor HILL's: precocious closure of the neural folds was a possibility to be remembered, and the dual nature of neural crest ectoderm was quite likely.

Drs W. J. STRAUS and G. WEDDELL read a paper on "The earliest reactions of mammalian skeletal muscle to electrical stimulation of measured frequency".

Living foetuses of the white rat were used. The parents were given Nembutal subcutaneously and the foetuses investigated with the placental circulation intact, in a bath of physiological saline maintained at approximately 37° C. The first stimuli used were derived from an induction coil, but in later experiments this was replaced by a gas discharge valve delivering variable strength condensor shocks ranging in frequency from one shock per sec. to approximately 150 per sec. Bipolar electrodes were used.

The earliest responses were obtained from foetuses during the 16th day of gestation, measuring 13–14 mm. C.R. These responses involved the musculature of the forelimb only. The responsive musculature exhibited the following characteristics:

(1) Frequencies much below 90 per sec. were mostly ineffective.

(2) The threshold of stimulation tended to be high in the foetal muscle as compared with adult muscle.

(3) There was a definite latent period.

(4) Contraction was relatively slow.

(5) Contractions were not sustained, except in one specimen in which a "tetanic" contraction was produced by prolonged stimulation at a frequency of about 150 per sec.

(6) There was a tendency for rapid fatigue.

(7) Responses could only be obtained by repeated stimulation in some cases (Summation).

(8) Response in some specimens was more easily obtained by stimulation of peripheral nerves than by direct stimulation of the muscle.

Professor WOOLLARD spoke of the fundamental problems raised by the researches embodied in this communication, and of the necessity for the interpretation of present findings in accordance with present chemical ideas. Neurogenic responses preceded the myogenic; proprioceptive reflexes may precede cutaneous responses. Professor BEATTIE and Mr ROBINSON enquired concerning various technical experimental procedures, to which Dr WEDDELL replied.

Dr D. B. BROWN (introduced by Professor BLAIR) read a paper on "Macroscopic staining of the brain".

The improvements suggested by Mulligan were incorporated in the various macroscopic colouring reactions of the brain described by Blair, Davies and MacClelland. Further observations were made on the principles governing such reactions, including the most efficient method of fixation of the brain.

With the aid of these results a new staining method was worked out, using lead nitrate and silver nitrate plus ammonium sulphide. The specimens so obtained present an exaggeration of the natural colour differentiation between grey and white matter.

A simple cerebrotome was devised to facilitate the cutting of serial macroscopic sections of the brain.

Professor BLAIR said this paper showed that Zenker, and other brain-staining methods, are due purely to physical, not chemical, factors. The work of BLAIR and DAVIES was primarily directed towards the interpretation of such staining reactions and not to any attempt at establishing a permanent brain-staining method. Dr BROWN's present specimens had not faded after six months' full exposure to light. Professor DAVIES believed the present technique advocated to be an improvement upon all previous work; he suggested a modification to differentiate the phylogenetically older from the newer parts of the cerebral grey matter. Mr ROBINSON suggested silver sulphide as a better permanent colouring agent than lead sulphide. Dr BACSICH had found his own lead nitrate technique for brain staining inferior in its results to the present technique; he recommended glycerine-gelatine as a mounting medium. Professor WOOLLARD asked whether gelatine proved permanent as such a medium, as in his own experience it had proved very disappointing; he recalled the specimens stained and mounted over thirty years ago in Sydney by Professor WILSON, which had never faded or deteriorated in any way, due doubtless to two factors—the thorough washing of the specimens and the purity of the gelatine used in mounting. Dr BROWN replied, thanking members for suggestions, and giving details of his own method of mounting and displaying brain sections.

DEMONSTRATIONS

At this Meeting of the Society the following Demonstrations were given:

(1) Sir ARTHUR KEITH: Cast of the Florisbad skull.

(2) C. M. WEST: A mediaeval achondroplasic skull.

(3) A. J. E. CAVE: (*a*) A series of Neolithic crania. (*b*) Specimens illustrating growth-changes in vertebrae.

(4) T. NICOL: (*a*) Preparations illustrating fat distribution in the reproductive system of the virgin and pregnant cavy. (*b*) Preparations showing results of intra-vitam staining of the ferret uterus.

(5) J. M. McBRIDE (introduced by D. M. BLAIR): Autonomic neurogenesis in the chick.

(6) J. F. ROBINSON (introduced by J. P. HILL): Romanowsky staining processes.

(7) J. E. SEMPLE (introduced by J. BEATTIE): Innervation of the ureterovesical junction.

(8) D. M. BLAIR and D. B. BROWN: An improved cerebrotome.

(9) T. S. HESLOP (introduced by J. BEATTIE): Gastric motility produced by hypothalamic stimulation.

(10) J. BEATTIE and D. SLOME: Electrocephalograms.

(11) T. S. HESLOP and W. d'A. MAYCOCK (introduced by J. BEATTIE): Experimental demonstration of adrenal gland innervation.

(12) L. O'SHAUGHNESSY (introduced by J. BEATTIE): The provision of a cardiac accessory blood supply after coronary occlusion.

(13) G. A. G. MITCHELL: (*a*) Radiographic studies of intra- and extraperitoneal effusions. (*b*) Dissections of abdominal sympathetic nerves.

ANATOMICAL NOTES

SOME OBSERVATIONS ON THE PUBLICATION BY DR TIEGS ENTITLED "FURTHER REMARKS ON THE TERMINATIONS OF NERVES IN HUMAN TEETH"

By W. LEWINSKY AND D. STEWART

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In the course of the introduction to our paper on the Innervation of the Dentine, published in this *Journal* in 1936, we stated that Sealey (1932) had been able to trace nerve fibres into the dentinal tubules, but added that it was not quite clear from his description how far into the tubules he had traced these fibres. In describing the work of Tiegs (1932) we said that he

> was unable to trace the nerve fibres into the dentine but only as far as the subdentinal space, which he describes as a space between the odontoblasts and the dentine which is traversed by the dentinal fibres.

Tiegs, in his latest paper (1938), takes exception to these remarks of ours because he considers that Sealey's results do not differ from his own.

We feel that it is only fair to ourselves to make some observations on these remarks of Tiegs. No doubt a misunderstanding has occurred, and this is largely due to the use by Tiegs of the term subdentinal zone. In his original paper, Tiegs states:

> The inner margin of the dentine is very irregular and unfortunately is apt to stain very deeply. Immediately internal to this, in teeth that are not yet fully grown, is the odontogenic zone, imperfectly or not at all calcified, but with dentinal tubes already visible. Beneath this is a space (lymph space?) traversed by the processes of the odontoblast cells (Tomes' fibres), on their way to the dentinal tubes. This subdentinal zone of odontoblast processes is bounded on its inner margin by a peculiar membrane composed of collar-like attachments to the odontoblast processes....

In his plates, he also indicates the existence of both an odontogenic zone and a subdentinal zone of odontoblast processes and these are both very clearly illustrated in Figs. 1 and 3. However, in some of his other illustrations, no odontogenic zone is seen and only a subdentinal zone is present. From these drawings however, it appeared to us that in these latter instances the subdentinal zone was really the odontogenic zone. It was particularly in regard to these illustrations that we should have liked to have seen photomicrographs, then there could have been no possibility of any misunderstanding arising. As he fairly points out, other workers have cast doubts upon the existence of such a zone and we ourselves have never seen it. We therefore

felt justified in coming to the conclusion that Tiegs fibres had ended around the odontoblasts, and we were certainly justified in concluding that the fibres in question had not entered the odontogenic zone. However, as we have already noted, in some of his illustrations, the difference between "odontogenic zone" and "subdentinal layer" appears to be obscure and in our final summing up, we stated:

> **With regard to the findings of Tiegs, that the nerve fibres ended in the subdentinal zone, we must confess that we have never seen such a zone, but from his diagrams, it would appear that this was really the odontogenetic zone of the dentine, and if this is so, then the results which Tiegs obtained fall fully into harmony with those of other workers.**

That we were entirely justified in this conclusion is proved by Tiegs' latest paper, because herein he says in regard to the use of the term "subdentinal zone":

> **By this I mean the very narrow zone between the layer of odontoblasts and the inner margin of the calcified dentine. It is known by a variety of other names: odontogenic zone, dentogenetic zone, dentinoid zone, predentine, uncalcified dentine.**

If this account of the subdentinal zone be compared with Tiegs' earlier description which has already been quoted in this paper, it is quite obvious that the author has now included in the subdentinal zone the odontogenic layer. If therefore, any misunderstanding has arisen, it is due to this. At any rate, we feel that even with such a misunderstanding, ample justice was done to Tiegs' work by our statement that, if by subdentinal zone he meant odontogenetic zone, then his result was in harmony with those of Sealey and ourselves.

However, it is extremely satisfactory to us that this matter has now been cleared up and that there appears to be a consensus of opinion that the nerve fibres do go into the odontogenetic layer.

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THE ORIGIN OF THE M. PECTORALIS MINOR[1]

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During the progress of laboratory observations on a variety of anatomical features, records were collected on the origin of the pectoralis minor muscle. The results of this study are tabulated below; they represent 100 consecutive cadavers (200 muscles), whites and negroes; 97 were males, the remaining three females.

Table I. *Origin of the pectoralis minor*

	Ribs or costal cartilages of origin	Number of muscles	%
(1)	2–3–4–5 (Fig. *a*)	84	42·0
(2)	3–4–5 (Fig. *b*)	57	28·5
(3)	2–3–4 (Fig. *c*)	30	15·0
(4)	3–4 (Fig. *d*)	10	5·0
(5)	4–5	2	1·0
(6)	3–4–5–6	8	4·0
(7)	1–2–3–4–5	4	2·0
(8)	1–2–3–4	2	1·0
(9)	1–2–3–4–5–6	2	1·0
(10)	2–3–4–5–6	1	0·5
	Total	200	

As is regularly described, the muscle arises from the anterior ends of the ribs by aponeurotic slips which are continuous with the fascia covering the intercostal muscles (Fig. *a*). Most frequently (42 %; item 1 in Table I) these slips are attached from the second to the fifth ribs (Fig. *a*). But this origin may be reduced to three (Figs. *b* and *c*; 43·5 %, items 2 and 3) or even to two ribs between the costal limits mentioned (Fig. *d*; item 4, 5 %; item 5, 1 %). Thus 91·5 % of the pectoralis arose from all or some of the ribs between the second and the fifth. Cases whose origin extended beyond the territory of the second to the fifth ribs made up but 8·5 % of the total number (items 6–10, Table I).

[1] Contribution No. 272 from the Anatomical Laboratory of North-western University Medical School, Chicago, Illinois.

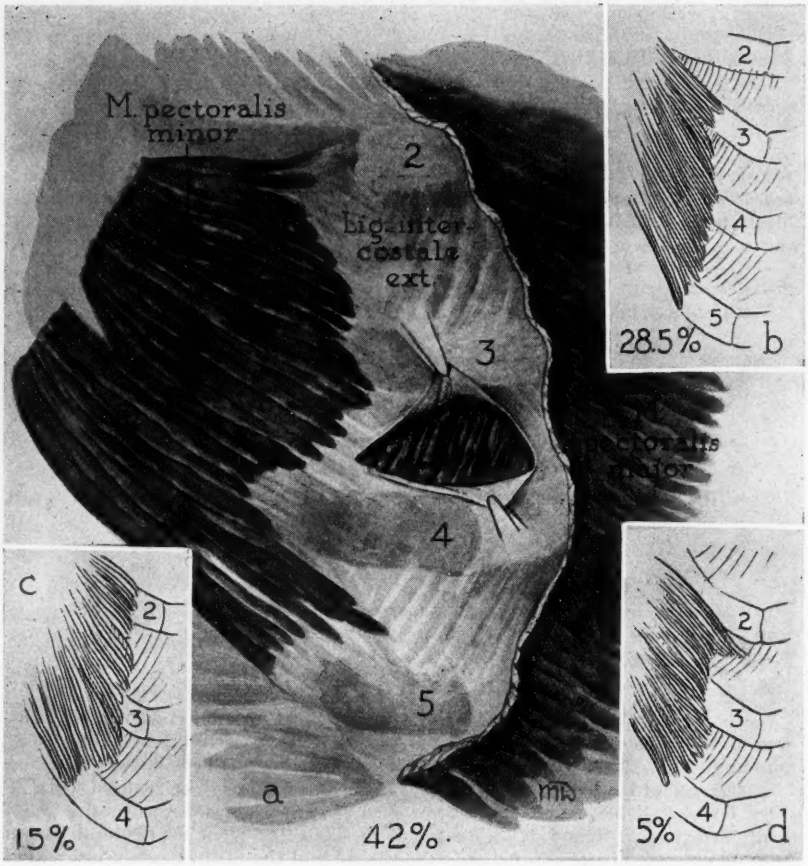

Fig. *a*. The right half of the thorax in the region of the upper five ribs; the pectoralis major muscle has been partially removed to expose the origin of the pectoralis minor. Figs. *b–d*. Types of costal origin. The occurrence of each is indicated by percentage. The cases illustrated represent 91·5% of the total number examined.

NOTE ON A MODIFICATION OF DELAFIELD'S HAEMATOXYLIN

By T. H. BURLEND and D. H. STRANGEWAYS

Department of Histology and Embryology (Anatomy), Cardiff

A series of tests has been made with the object of finding a haematoxylin stain for paraffin sections which requires no differentiation. The problem was suggested to us by Dr Quastel of the Biochemical Department of the Whitchurch (Cardiff) Mental Hospital, who felt that on theoretical grounds such a stain should be obtainable.

Our tests were made with Delafield's haematoxylin, but instead of using distilled water for making up the stain, buffer solutions of various hydrogen-ion concentration were tried. After numerous trials we selected Delafield's haematoxylin made up in a buffer solution of *p*H 1·7.

The buffer solution and the stain are made up as follows:

*Buffer solution p*H 1·7

0·2 *M* KCl	100 c.c.
0·2 *N* HCl	43 c.c.
Distilled water	257 c.c.

(0·2 *M* KCl contains 14·9 g. KCl in 1000 c.c. distilled water: 0·2 *N* HCl contains 7·3 g. HCl in 1000 c.c. distilled water.)

Haematoxylin stain

Haematin	3·2 g.
Ammonia alum	6·8 g.
Buffer solution *p*H 1·7	350 c.c.
Glycerine	75 c.c.
Absolute ethyl alcohol	75 c.c.

(10 g. of Gurr's Delafield's haematoxylin powder may be used instead of the haematin and ammonia alum.)

The haematin and ammonia alum are dissolved in the buffer solution by gentle heating; the glycerine and alcohol added when the solution is cold. The stain can be used immediately after being made up, and it keeps well. We have noted no deterioration in stain made up in July 1936.

Paraffin sections are down-graded to water and stained in the haematoxylin for 3 min. or longer. Times varying between 3 min. and 24 hr. were tried, and it

was found that the length of time of staining made no appreciable difference. After staining, the sections are well washed in distilled water and exposed for 1 min. over a jar containing 5 % ammonia so that a blue stain results. (When many sections are being stained at the same time, the frame containing the slides should be held in the ammonia vapour and not allowed to come in contact with the liquid ammonia.) After dehydrating, the sections may be counterstained in a saturated solution of Chromotrop 2R in absolute alcohol for 2–3 min. Other counterstains producing a good contrast may be used.

Ammonia vapour is preferable to either tap water or lithium carbonate, as it gives a sharper and cleaner result. A very nice nuclear stain is obtained without the ammonia treatment, but in this case it is difficult to get a good contrast counterstain. Picro-indigo-carmine is a satisfactory counterstain when the sections are not rendered alkaline, but it tends to take out the haematoxylin stain. The stain gives equally good results with tissues fixed in formalin, Zenker, Bouin, Susa, alcohol and corrosive sublimate.

The great advantage of using the above formula for the haematoxylin stain lies in the fact that there is no appreciable overstaining if the sections are left in the stain for a number of hours; in consequence no differentiation is necessary. In the hands of students with a limited experience, who are apt to overstain or overdifferentiate, and for routine laboratory preparations, we have found the stain highly satisfactory.

THE SEXING OF THE HUMAN SACRUM

By EDWARD FAWCETT

In the year 1931 I had come to the conclusion that there was a fairly easy method of sexing the sacrum which is not so far as I know given in any of our textbooks. The method I suggested is a very reasonable one in that it consists of comparing the transverse diameter of the first sacral vertebra with the transverse diameter of the base of the sacrum. From what one knows of the comparative slenderness of the female Lumbar column one cannot be surprised if the transverse width of the first sacral vertebra harmonizes with the narrowness of the centra of the Lumbar vertebral bodies in the same sex.

Not having the material necessary at my disposal I wrote to Prof. Wingate Todd who with his usual kindness at once set in motion an investigation which he entrusted to Mr William Sassamen. The results are of great interest.

The following samples and age range were used.

$$\frac{CW \times 100}{BW} = \text{index of body.}$$

CW is corpus width; *BW* is basal width.

	White races		Coloured	
	Male	Female	Male	Female
Number in sample ...	134	79	108	88
Age range	25–49	22–54	25–48	23–52
	Corporo-basal index			
Range	37·606–54·91	33·777–49·506	40·271–56·650	35·217–50·0
	17·304	15·809	16·379	14·783
Mean	45·041	40·486	48·635	42·395
P.E. of mean	±0·184	±0·276	±0·213	±0·249
S.E. of mean	±0·273	±0·410	±0·316	±0·370
Median	45·000	40·437	49·015	42·375
Mode	44·918	40·339	49·775	42·335
Stand. Dev.	3·170	3·645	3·289	3·471
St. Er. St. Dev.	±0·193	±0·289	±0·223	±0·261
Coeff. of var.	7·030	9·000	6·760	8·180
Skewness	0·138	0·040	0·346	0·017

P.E. of mean is probable error of mean.
S.E. of mean is standard error of mean.
Stand. Dev. is standard deviation.
St. Er. St. Dev. is standard error of standard deviation.

It is quite clear from the above table that the surmise as to the sexing value of a corporo-basal index is justified. Wingate Todd in his letter to me conveying the results of the investigation speaks of the results as so illuminating that they should be published as soon as possible. That this was not done was the result of a misunderstanding.

My best thanks are due to Prof. Wingate Todd for causing this investigation to be made.

THREE CASES OF FUSION OF AXIS WITH THIRD CERVICAL VERTEBRA

By Y. H. AASAR
Cairo

Recently Cave (1937) reported on some sixty-two cases of fusion of the axis with the third cervical vertebra; he emphasized the normal limitation of movement between these bones, termed the third vertebra the "vertebra critica" and interpreted fusions of the axis with this vertebra as attempts at the formation of a functional cervical "sacrum". Borovansky (1928) discussed the same subject, and noted that the minimal spinal mobility obtaining between the second and third cervicals disposes towards their fusion, as evidenced in various mammals.

The three specimens herein described reveal various phases of this particular variety of vertebral synostosis.

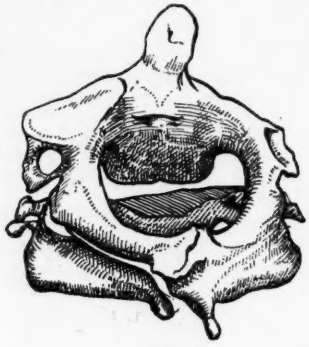

Fig. 1.

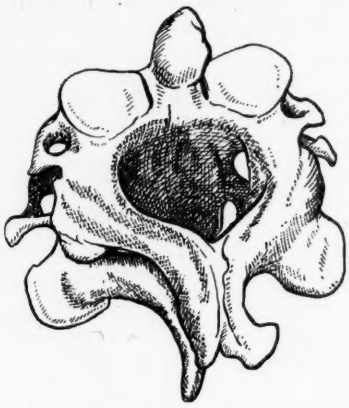

Fig. 2.

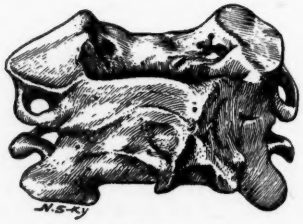

Fig. 3.

Fig. 1. Fusion of second and third cervical vertebrae in a child of 12. Fusion is partial, and the third spine is double.

Fig. 2. Fusion of second and third cervical vertebrae in an adult. Fusion practically complete.

Fig. 3. Fusion of second and third cervical vertebrae. Absence of odontoid; modified superior articular surfaces of axis (suggesting occipito-atlantal synostosis).

Case 1. The specimen (Fig. 1) is from a child about 12 years old, judging by the degree of coalescence of the apical odontoid epiphysis. The neural arches and articular processes of the axis and third cervical are completely fused on the right; otherwise the two vertebrae remain independent. The hemi-arches of the third cervical vertebra have failed to unite dorsally; a condition of spina bifida results, each hemi-arch bearing its own spinous process; the right third hemi-arch is intimately synostosed with that of the axis vertebra.

Case 2. The specimen (Fig. 2) is from an adult column. The axis and third vertebra are almost completely fused. The bodies are indistinguishably fused dorsally, but on the right side only ventrally. The right neural arches and articular processes are completely synostosed, as are the left articular processes; the left laminae are almost completely fused. The third spinous process is double and asymmetrical, its right moiety being incorporated into the under aspect of the overhanging bulky spine of the axis.

Case 3. This specimen (Fig. 3) is more interesting. The second and third cervical bodies are fused on their extreme left, fusion being more pronounced dorsally than ventrally; the gap between their free portions is wider ventrally than dorsally. The neural arches, articular processes and spines are completely fused on the left side and almost completely so on the right. An outstanding feature of this specimen is the absence of the dens and the rather reniform configuration of the axial superior articular processes. (Unfortunately, the remainder of this cervical column is not available.) It is known that the odontoid process may, though extremely rarely, remain distinct, and that normally the odontoid unites with the axial neural arch before uniting with the axis centrum. Whether the separate atlas centrum (odontoid) has, in this case, remained independent, or has fused with the occipital bone, cannot be determined. That the atlas itself, in this specimen, had fused with the occipital is strongly suggested by the reniform (i.e. pseudo-atlantal) nature of the superior articular processes of the axis. For in about one-half of such fusions the inferior atlantal articular processes assume a reniform, pseudo-condylar, configuration, necessitating a corresponding morphological modification of the superior axial processes, to meet the demands of altered function.

I am indebted to Prof. D. E. Derry for his help and to Mr Strekalovsky for his drawing.

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REVIEWS

Practical Neuroanatomy. A Textbook and Guide for the Study of the Form and Structure of the Nervous System. Adapted to the needs of students and practising physicians. By J. H. Globus, B.S., M.D. (London: Baillière, Tindall and Cox.) 1937. xxii + 387. 92 figs. 55 Pl. Price 27*s.* net.

The earlier form of this book kept more closely to the intention of serving as a manual of practical neuroanatomy. The present issue adds further chapters and commentaries which make it a textbook of Neurology as well. The original plan of the book remains, but the short literature lists and suggestions for essays included in the former text have now been omitted. We regret the omission of this admirable feature of American teaching.

The text is based mainly upon the use of the method of dissection, the staining of tracts by means of the Weigert methods, the identification of nuclear masses, and the use of the special methods for nervous tissue. A short chapter describing these has been included.

The earliest exercises are concerned with the brain after its removal from the body, and thus the student begins with the meninges, the external aspect of the brain, and the arrangement of the blood vessels. From this beginning all the central nervous system is passed in review until the spinal cord is reached. The stages in the practical work are subdivided into an orderly and progressive series of "assignments" of convenient size. Of these there are twenty-five, and each includes a descriptive text, instructions for the guidance of the student and appropriate drawings, diagrams and sketches. The last assignments are devoted to nerve cells, neurones, neuroglia, and the like.

After the conclusion of the practical work the second part of the book assembles together, in functional groups, the organs, tracts, nuclei, etc., described in the practical part and thus makes a summary of the structure and functions of the central nervous system. The value of this is emphasized by the inclusion of a series of clinical cases, the elucidation and understanding of which depend on a knowledge of the anatomy herein described and analysed.

The needs of the student and the teacher also are subserved not only by the convenient division of the work into assignments with appropriate text and figures (some ninety-two in all), but also by the inclusion of an index and some fifty-eight detachable outline drawings. These outlines enhance the accuracy and usefulness of the student's own record and increase the time available for observing and learning.

The book is certainly a most valuable addition to resources of anatomical teaching.

An Introduction to Physical Anthropology. By E. P. Stibbe. With an Appendix by W. A. Smart. 2nd edition. (London: Edward Arnold and Co.) 1938. Pp. vii+230, 56 figs. Price 10*s.* 6*d.* net.

A second edition of *An Introduction to Physical Anthropology* has now appeared. The time has passed when physical anthropology could be adequately presented in a few brief chapters of a work on general anthropology. Since those days there has been great progress not only in the description, tabulation, and assessment of the physical characters of modern man, but also in those dependent and related realms of knowledge such as human palaeontology, comparative anatomy of primates, ethnological history and prehistory, and particularly in genetics and biometry. The

author has made an attempt to correlate these branches of knowledge in a book which the student is to use in the early days of his study.

There are statements in this volume which will be classed by one or other expert as inaccurate. One finds it stated that the "orang-utan...grows to the size of man"; that the beard of the Arab, Ethiopian, and Hebrew is "very strong"; and that the Australian aborigines are "very short" in stature. Criticism might come from the geneticists complaining that the bearing of the gene theory on physical anthropology has not been presented. However, the facts put forward are of practical value, and the author has retained with this practical utility a breadth of outlook. The appendix on statistical methods is a useful addition to this revision of the book.

The Structure of the Fowl. By O. CHARNOCK BRADLEY. (Edinburgh: Oliver and Boyd.) 2nd edition, 1938. Pp. xi+139. 75 figs. Price 7*s.* 6*d.* net.

In the small compass of 133 pages which include 75 clear figures the author has given a concise and lucid account of the anatomy, microscopic and macroscopic, of the domestic fowl. This second edition of Dr Charnock Bradley's book, while containing more illustrations than the first, and though re-written in many sections, has not lost any of its advantages of accuracy and simplicity of expression. A succinct account of the development of the chick considerably enhances the value of the book.

It will certainly continue to serve very satisfactorily the requirements of students and others in a number of fields. By insistence on the important facts of the anatomy and by continuing to avoid excessive detail in the second edition Dr Bradley has ensured the practical utility of this work.

The Treatment of Clinical and Laboratory Data. By DONALD MAINLAND, M.B., Ch.B., D.Sc. (Edinburgh: Oliver and Boyd.) 1938. Pp. xi+340, with 23 text-figures. Price 15*s.* net.

The subtitle of this book describes it as "An Introduction to Statistical Ideas and Methods for Medical and Dental Workers". The description is true. This book does give a simple, accurate, and helpful introduction to statistical methods and ideas, with examples drawn from anatomical, physiological, pathological and clinical sources. That in itself is half the battle; for the chief difficulty with earlier introductions to statistics has been that the anatomist who was not at home in the subdivision of morphology called mathematics was asked to acquire an unfamiliar subject illustrated by examples drawn from equally unfamiliar fields of work. Prof. Mainland begins with an interesting chapter on the objects and method of study of his book. The later chapters deal successively with the comparison of qualitative data, quantitative data, errors in measurement (as distinct from natural variation), and finally with correlation of characters. Each chapter is concluded by a list of books and papers which deal more fully with special points, the references being completed by a bibliography at the end of the book. The table of contents is most clearly set out, a model of its kind, and there is a fairly full index.

A few points could well receive Prof. Mainland's attention in the preparation of a second edition. Some account of the symbolism of modern statistics could well find a place in appropriate chapters, as well as in a comprehensive list at the end of the book; for example, signs of summation, use of subscripts, the reading of such terms as *rows* and *columns*. If this book fulfils its purpose, as it is fit to do, it will drive the fledgling medical statistician to such more detailed accounts of the arithmetic of variation as that of L. H. C. Tippett (*The Methods of Statistics*, 1937) or of R. A. Fisher (*Statistical Methods for Research Workers*). The chief difficulty of these books is the wide use made in them of such general terms as have been indicated

above. The coefficient of correlation (r) might receive rather fuller treatment, and its fundamental connexion with the variance of the correlated characters made quite clear. Lastly, it is possible that at least the greater part of Chap. VII (on publication of results) could be put into the first chapter, of which the seventh is the logical continuation.

Die Feinsten Blutgefässe des Menschen. Erster Band. Prof. Dr OTFREID MÜLLER. (Stuttgart: Ferdinand Enke Verlag.) 1937. Pp. xx+745, 207 figs. Price 55 RM.

Prof. Otfried Müller has assembled in the first volume of this work a great mass of facts and theories relating to human blood capillaries. The task has been done with such thoroughness that the volume will surely serve as the standard reference for many years to come. One is struck by the very large number of fine photographs and coloured plates showing the living capillaries in all the accessible regions of the body surfaces and under diverse conditions. Most of these are the result of work done under Dr Müller at the Tübingen clinic. The simple lucid style of writing, combined with clarity of thought, has produced an ordered sequence of well-paragraphed sections through which anyone can readily find his way. The work covers the whole range of knowledge of human blood capillaries, their embryology, structure, topography, mechanics, physiology, biochemistry, pharmacology, and the applications of these to pathology and clinical states.

Two-thirds or so of this volume, i.e. about 500 pages, is devoted to a general account of the aspects of the subject mentioned above, while the remaining 200 pages present detailed accounts of the capillaries of the various special tissues and organs of the body. Every minor and major fact of the physiology and anatomy of the capillaries has been worked out by direct study of the living human skin, and Prof. Müller has provided a complete encyclopaedia in which one may find an answer to such questions of capillary pattern, or (say) precise rates of capillary blood flow, or exact effects of this or that mechanical stimulus to the capillary wall. In spite of the wealth of detail the main principles stand out clearly, thanks to the excellent editing and illustrations. The fundamental work of such men as Sir Thomas Lewis and Krogh dominates the text and is well illustrated.

In the second part of the volume the best anatomical illustrations have been collected to show the vascular patterns of the organs, and the same exhaustive thoroughness is given to discussion of the special functional problems of each capillary bed. Only in this section may one find sometimes a perhaps incautious acceptance of work which might be viewed a little more critically. For instance one feels that if Pfeifer's account of the cerebral vessels is to bulk very large then the deficiencies as well as the advantages of the methods he used might be discussed. In this second section the urge to find functional significance in every topographical peculiarity would seem to lead the author at times somewhat into the path of speculation.

Great learning, patient industry, and clarity of presentation have made this a valuable encyclopaedia.

Handbuch der Anatomie des Kindes. Edited by Drs KARL PETER, GEORG WETZEL and FRIEDRICH HEIDERICH. Vol. I, Part 4. (Munich: J. F. Bergmann.) 1936. Pp. 525–628. RM. 24.

This part of the *Handbuch der Anatomie des Kindes* is devoted to the respiratory apparatus. Prof. Peter deals with the larynx and Prof. Wetzel with the trachea, bronchi and lungs. As in the parts of this handbook previously published, the

embryology of the organs is described and in turn the anatomical features at the various ages from birth to puberty are clearly traced. A feature of the section dealing with the larynx is the efficient arrangement of a series of tables in which the dimensions of the organs are given. The changes in the character and distribution of the lining epithelium are well presented. In the second part the growth changes in the lungs are carefully traced, and numerous tables present the dimensions of trachea, bronchi and lungs. The lymphatic glands of the lungs and bronchi are well portrayed but there is no adequate description of the right-sided paratracheal glands which so frequently give rise to symptoms in childhood.

Handbuch der Anatomie des Kindes. Edited by Drs KARL PETER, GEORG WETZEL and FRIEDRICH HEIDERICH. Vol. II, Part 5. (Munich: J. F. Bergmann.) 1938. Pp. 845–928. RM. 12.60.

The final part of the second volume of this handbook is a summary of the main characteristics in the growth of the child from birth to adolescence. Profs. Wetzel and Peter have concentrated into 70 pages all the essential features in the growth of the child. The synopsis is easy to follow as for each stage from the newborn, suckling, infant, school child, male and female adolescent, separate paragraphs are devoted to growth, skeletal and muscular, blood-vascular, alimentary, respiratory, urogenital, endocrine, nervous systems. Special paragraphs are devoted to the special sense organs, the organs of internal secretion, and the skin.

The section dealing with the anatomy of the newborn is followed by two sections devoted to the anatomy of the premature child and the anatomy of the child during the neonatal period.

No student of anatomy, physiology or paediatrics can afford to be without this collection of data. Anyone interested in the problems of child behaviour would be well advised to consult this summary before making any statements on the anatomical or physiological basis of the pattern of behaviour in the child.

The Development of the Vertebrate Skull. By G. R. DE BEER. (Oxford University Press.) 1937. Pp. 550, 143 plates. 30*s*.

Dr de Beer in this book provides a comprehensive summary of all research on the development of the vertebrate skull from the lamprey to man. Few people are better qualified to undertake this formidable task than Dr de Beer, who has been actively engaged on the morphological side of this subject for more than fifteen years. A glance at the length of the bibliography immediately gives an idea of the enormous amount of literature on which he has drawn. The author's object in writing such a book is to give "a systematic description (of the skull development) of all the Vertebrate types using a uniform nomenclature and stressing the points of comparison as far as possible", and it is the author's hope "that this book may be consulted with profit by Vertebrate morphologists, palaeontologists and human anatomists".

The book is extremely welcome as it provides a far more detailed and exhaustive account of the comparative embryology of the skull, especially the development of the cartilaginous parts, than has hitherto been published or for that matter is likely to be published again. The trend in embryological research at the present time is away from mere description and phylogenetic speculation to the study of the causes underlying development and the processes responsible for the ultimate form of the adult. For this very reason Dr de Beer's book is an invaluable contribution and it will in all probability be the final summary of the descriptive embryology

of the skull, on which the experimental research of the future will be based. In this respect the skull has been a relatively neglected field, in which many interesting avenues of research are obvious.

In addition to the merely descriptive part of the book, which is excellent, there is a comparative section and a general section. Amongst other things the latter deals with the phylogeny of the chondrocranium, the growth of the skull, causal relationships in the development of the skull and ends with an agenda suggesting forty-five special problems for future investigation. It is this part of the book which will be of the greatest interest to the general biologist. In the agenda, in which suggestions for future research are given, the reader will be particularly struck by the way in which the problems fall into two main classes, those which are intended ultimately to be of phylogenetic value and those which are concerned with the processes of development. For example, many of the problems are intended to help elucidate the fundamental question of what determines the limitations and sutures between bones generally and what are the factors governing their size and number. The author appreciates the importance of this problem, as can be seen in his very interesting discussion on the identity of morphological units. This section raises the question of "what is a bone?" and the author finds himself unable to supply a satisfactory answer in the present state of our knowledge. In fact he comes to the conclusion that one cannot define any particular bone. Since such a definition is basic to all bone comparisons, it seems rather illogical any longer to enter into detailed discussions of bone homologies. The table given on pp. 500 and 501 illustrates the difficulty of such comparisons and the danger of making them. Very few workers would agree that the bones compared are homologous or rightly identified, since none of them has any really clear definition of what such terms as "intertemporal" and "supratemporal" actually mean.

The value of the skull as evidence for unravelling the phylogeny of the vertebrates is enormous, but in this connexion the development cannot be divorced from the adult form. The author treats the phylogenetic significance of the skull only from the standpoint of embryology and makes it clear that the conclusions drawn are comparatively unimportant. For example, in the face of the evidence of palaeontology it seems pedantic to require additional support for such views that the mammals are derived from reptiles, or that the sturgeon is not closely related to the elasmobranchs! This only emphasizes to the reviewer the importance of the fact that the future of embryology lies in the study of causes underlying form and that the study of phylogeny must be left to palaeontologists.

In conclusion the author must be congratulated for the comprehensive way in which he has marshalled so much literature, and the Oxford University Press for having published a book so beautifully produced and so rich in illustrations for the comparatively small sum of thirty shillings.

Atlas of Skeletal Maturation, 1926–1936. By T. Wingate Todd. (St Louis: The C. V. Mosby Company.) 1937. Pp. 203, 75 plates. Price $7.50.

By definite recognizable stages the developing organism passes from its beginning as a fertilized ovum to its maturity, senescence, and death. The growth curve has been plotted for all kinds of living things, including members of the vegetable kingdom. The curve rises steeply at first, but the acceleration diminishes after birth. In man there is a slight spurt in the early years of childhood and, of course, another very considerable one at puberty. Thereafter the curve slowly flattens out into the equilibrium of maturity.

Of course the curve for the organism as a whole is not the same for all the anatomical systems which compose it. The behaviour of the nervous system, the

gonads, the reproductive system, and the lymphatic system offer the greatest contrast. Volume, weight, and stature have naturally been the most common measures of growth. They are not altogether suitable. They are at once too precise and too crude. Though weight can be measured most accurately, yet without other enquiries it cannot be known whether the increase is due to normal growth or the accumulation of fat from wrong feeding and bad hygiene. Thus there has always been the search for some better measure, not only of the increase of tissue, but also of the orderly progress of differentiation that ends with maturity. Further it has always been hoped that a system, which permits of accurate measurement and which is also an excellent indicator of growth, differentiation, and the degree of maturation, might also serve as an index of the same events occurring in other systems of the body inaccessible to observation and incapable of precise measurement.

The study and the recording of changes by the radiographic method has, of course, attracted a large number of anatomists and others to the study of growth and differentiation as they unfold themselves in the bones. The apparent simplicity and ease of using, say, the hand region for such a purpose is as deceptive as it is attractive. To carry it out requires great resources, endless patience, and co-operation. The technical side demands the greatest care if pictures comparable with one another are to be obtained, and it requires great skill and experience to decide eventually what the pictures mean when you have got them.

The achievement which culminated in the publication of the present *Atlas* represents the repeated examination of a quarter of a million of radiograms, the handling of doctors, parents and children—some four thousand and more persons—so that they may give their willing co-operation, the organization of an X-ray department to take these pictures accurately according to the best possible standards, the naming and recording of the subjects of the radiograms, along with all the other relevant information such as age, sex, economic circumstances, complete medical history, etc., and finally the evaluation of each picture.

Prof. Todd and his collaborators have set themselves the task of acquiring by means of these methods standards which will serve as a time-clock of maturation. This radiographic clock has been subjected to every test by means of which its accuracy could be tested and from them all it emerged triumphant. Thus we can take these standards of the Atlas and measure against them any radiogram of the hand in the growing period of life. Economic circumstances, disease, vitamines, present and past record of health, etc.—all have been considered. We now have a tabulated succession of standards, thirty-nine in number for males and thirty-five for females, which the bones of the hand and wrist in a normal person reach for every three months in the first year of life and every six months thereafter until the skeleton is mature.

Everyone who believes that science progresses by making accurate measurements, who desires an accurate measure of growth and of differentiation, who wants to record differences in maturation from any cause whatever, will have reason to be grateful to Prof. Todd and his collaborators, who created and maintained the necessary resources, who by unceasing self criticism acquired the essential knowledge and skill, and who by their untiring labours gave to the world this *Atlas of Skeletal Maturation.*

Dixon's Manual of Human Osteology. Revised by E. B. Jamieson. 2nd ed. (Oxford University Press.) 1937. Pp. ix+465, 180 figs., 28 plates. Price 21*s.* net.

The scope of the first (1912) edition of the late Prof. Dixon's classic manual was somewhat strictly confined to pure descriptive osteology, mention of soft parts being limited to those muscular and ligamentous structures associated with the morphology of individual bones.

In this new edition, osteology has been interpreted in more liberal fashion and detailed description is made the key to the ready understanding of much non-skeletal anatomy. No effort has been spared to modernize an excellent and established treatise, at the same time conserving the essentials of its original character. The rewritten and greatly augmented text has been enhanced in usefulness to the student by the substitution of the Birmingham for the Basle Nomenclature and by the copious inclusion of explanatory etymological notes. The former brief account of bone histology and development has been greatly amplified, radiographs and new figures (mainly from Cunningham) have been incorporated, and particular stress has been laid upon surface anatomy.

Illustrations of Regional Anatomy. By E. B. JAMIESON, M.D. Sections I–V. (Edinburgh: E. and S. Livingstone.) 1937. Sect. I. Central Nervous System, 48 plates. Price 7*s.* net. Sect. II. Head and Neck, 63 plates. Price 12*s.* 6*d.* net. Sect. III. Abdomen, 37 Plates. Price 5*s.* 6*d.* net. Section IV. Pelvis, 33 plates. Price, 3*s.* 6*d.* net. Sect. V. Thorax, 30 plates. Price 4*s.* net. Price complete set, 32*s.* 6*d.*

The present five sections complete Dr Jamieson's atlas of regional anatomy. Opinions will necessarily differ concerning the desirability and utility of such atlases, the relative importance of included or excluded matter and the respective merits of pure diagram and finished plate. The author has, however, steered a middle course, being guided in his selection of illustrations by a long and intimate experience of the difficulties of the student. The student will find the plates an excellent aid to rapid and profitable revision.

Short Manual of Regional Anatomy. By J. A. KEEN, M.B. (Lond.), F.R.C.S. (Eng.). (London: Longmans, Green and Co., Ltd.) 1937. Pp. 167, 75 figs. Price 5*s.* net.

This synopsis of regional anatomy is planned upon the familiar lines of a "pocket anatomy" with the inclusion of selected conventional diagrams.

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